ECOLOGICAL INVESTIGATION OF SOME SUBALPINE TREES AND SHRUBS

A thesis
submitted in partial fulfilment
of the requirements for the Degree
of
Doctor of Philosophy in Botany
in the
University of Canterbury
by
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University of Canterbury
1985

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A B S T R A C T

Measurements and observations of plant morphology, growth and reproduction of four subalpine trees and/or shrubs, the deciduous *Hoheria glabrata* and the evergreen *Olearia ilicifolia, Senecio bennettii* and *Dracophyllum traversii* were carried out at Arthur's Pass National Park. Climate records and soil data provide an outline of the general physical environment in the sites occupied by these species.

It was verified that the mosaic-like occurrence of forest and scrub stands dominated by each of the four species is mainly related to a gradient of declining soil fertility. This fertility gradient is reflected by increasing podzolization of the soil profiles, decreasing element content of the respective plant tissues, and inherently slow growth rates of the species occupying the more mature soils.

Hoheria and *Olearia* colonize recently disturbed sites, *Senecio* regenerates under the forest canopy but is more successful than *Hoheria* and *Olearia* in open ground in the course of secondary succession. The latter also applies to *Dracophyllum*.

Shoot elongation and leaf area increment is concentrated into a short flush early in the season in *Hoheria* and *Olearia*, but extends from August to May in *Dracophyllum*. The considerable seasonal variation of both leaf area and shoot growth is unrelated to the climatic quality of the current season. *Hoheria, Olearia* and *Senecio* form resting buds and temperatures during the period of leaf primordia initiation predetermine the number and size of leaves of the subsequent growing season. *Dracophyllum* does not form resting buds and leaf area growth is related to the quality of the current

season.

Flowering is annual, but except for *Hoheria* and *Olearia*, only a part of the population is involved each year.

Though vegetative growth stops during the winter months, and annual growth layers are formed in the wood, the evergreens are not entirely dormant, and flower bud development, litterfall and even wood increment may continue in some species.

C H A P T E R I

I N T R O D U C T I O N

1. GENERAL REMARKS ON THE GEOECOLOGY OF SUBALPINE WOODY VEGETATION.

The growth of trees and tall shrubs in the high latitude subpolar zones as well as in the subalpine belts of high mountains is restricted by low summer temperatures and the long duration of the winter snow cover. The upper (northern/southern) boundary of the belts or zones characterized by tall woody plants is the timberline. Subalpine vegetation belts can be found anywhere on the globe where mountains rise to elevations that sufficiently reduce air temperatures. Three major subalpine (and alpine) vegetation regions have so far received the particular attention of ecologists and plant geographers; the tropical high mountain regions and the two subalpine belts in the northern and southern temperate zone. Here climates are humid enough all year round to allow for the growth of closed forests from sea level to timberline. The subalpine vegetation of the northern temperate zone is well known to botanists and plant geographers; most mountain systems are situated in regions with continental climates, i.e., the seasons are well marked, the winters cold and with considerable snowfalls. Subalpine woody vegetation is characterized by the prominence of conifers; only a few deciduous species like *Alnus*, *Betula* or *Salix* may be present as well. Evergreen dicotyledons only occur as dwarf shrubs (e.g. *Arctostaphylos*, *Daphne*, *Empetrum*, *Ledum*, etc.), and can only grow in places where they become completely covered

by winter snow. The harsh winter climates seem to have been strongly selective in respect of tree life. On the other hand, plant geographers have sometimes stressed certain similarities in ecology, physiognomy, and to some extent in floristics, of the vegetation of the tropical high mountains and the southern temperate zone (e.g. Troll, 1960; 1973). These relationships are partly a result of the common geological history of the southern continents as part of Gondwanaland, but also due to certain similarities in respect of the prevailing climatic conditions. Tropical mountain climates are strictly diurnal without any noticeable seasonal temperature variation. Climates of the southern temperate zone are largely influenced by the particular geography of the southern hemisphere. As compared with its northern counterpart, the southern temperate zone has a very restricted land area resulting in the prevalence of oceanic climate regimes. Furthermore, most of the lands of southern middle latitudes are characterized by high mountain chains causing local climates of an extremely oceanic superhumid type, i.e., seasonal variation is of a much lower order than in the northern hemisphere, and precipitation is high throughout the year (compare relevant climate diagrams in Walter, 1971; 1977). This is particularly true for the western regions of New Zealand. It has therefore sometimes been questioned - mainly on the basis of vegetation physiognomy and floristics - whether the seasonal or diurnal temperature variation would be more prominent (Troll, 1943; Schweinfurth, 1966). Troll (1948) went so far as to suggest an all year round growing season for New Zealand subalpine vegetation. He still seems to hold to this idea in his 1973 paper (Troll, 1973; p.A16), though P.Wardle had, in the meantime, clearly demonstrated

seasonal growth for New Zealand woody subalpines (Wardle, 1963a). Though Schweinfurth (1966, p. 245) recognizes Wardle's results, he still remains sceptical, because Wardle's growth measurements had been carried out at Broken River, an area well east of the Main Divide with a less oceanic climate and thus a more distinctly seasonal one.

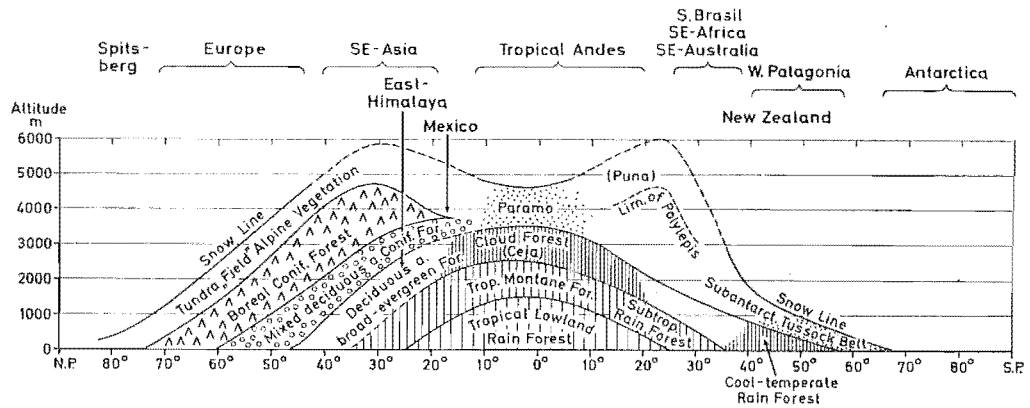

Figure 1. Schematic vegetation profile of the world, showing asymmetrical altitudinal belts in the humid regions (from Walter, 1971).

In the New Zealand South Island subalpine woody vegetation other than that dominated by beech (Nothofagus spp.) develops its greatest diversity west of the Main Divide in the region of the so called "beech-gap" between the Taramakau and Karangarua Rivers of Westland. This plant formation, commonly called subalpine scrub, harbours a variety of woody plants ranging in stature from tall trees (e.g. *Libocedrus bidwillii**) and larger shrubs (species of *Olearia* and *Senecio*) to dwarf shrubs and creeping shrubs such

*Nomenclature follows Allan (1961) except for Araliaceae (Philipson, 1965).

as species of *Gaultheria* and certain Coprosmas. The floristic inventory is mainly recruited from four different groups of species:

a) Trees and shrubs of the lowland to montane rainforest that decrease in stature with increasing altitude, e.g. *Griselinia littoralis, Metrosideros umbellata, Pseudopanax simplex.*

b) Species from lowland to montane habitats with a high incidence of disturbance, e.g. *Hebe salicifolia, Hoheria glabrata, Olearia avicenniaefolia, Olearia ilicifolia.*

c) Species that occur on "difficult" sites at lower altitudes, usually on nutrient deficient soils, e.g. *Libocedrus bidwillii, Phyllocladus alpinus, Dacrydium biforme.*

d) Species with a predominantly montane to subalpine distribution; *Dracophyllum traversii, Olearia colensoi, Olearia lacunosa, Senecio bennettii, Podocarpus nivalis.*

Table 1. Altitudinal vegetation belts in New Zealand at latitude 43°S (after Wardle, 1960; 1964).

1500m	----------
	high alpine
1200m	----------
	lower alpine
900m	----------
	subalpine
600m	----------
	montane
300m	----------
	lowland
s.l.	----------

The physiognomy of the subalpine scrub is characterized by certain life forms that are exhibited by members of varied taxonomic origins. Species of *Olearia, Metrosideros* and *Pseudopanax* show the growth habit of the "spherical umbrella tree" (Kugelschirmbaum) described by Troll (1948) from the tropical high mountains. Woody plants of lower stature often reveal the same growth habit in the form of spherical shrubs (Kugelbusch), well exemplified in *Olearia colensoi, Senecio bennettii, Senecio bidwillii* and *Pseudopanax colensoi*. Tuft trees like *Dracophyllum traversii* are another remarkable feature, also reminiscent of warmer climates, and the indigenous *Libocedrus bidwillii* seems closely related in appearance and ecology to the montane to subalpine *Papuacedrus* in New Guinea (Wardle, 1973).

The general notion concerning the altitudinal range of a plant species is that its upper limit is caused by increasing physical stress and the lower limit of distribution is regarded to be the result of biological competition. At higher altitudes a species may escape this competition from the lowland vegetation but has to cope with cooler temperatures, reduced solar radiation because of a high incidence of cloudiness and a generally shorter growing season. What enables the woody species of the New Zealand subalpine scrub to cope with the environmental conditions prevailing at higher altitudes? Was it necessary for them to possess or develop a common specialized life strategy or could they successfully employ different inherent life strategies which had evolved in lowland habitats?

In fact, at the altitude of the subalpine belt west of the divide, winter frosts are not severe and are usually

restricted to the early morning hours; only a few days reveal mean temperatures below $0^{o}C$. On the other hand, occasional night frosts may occur throughout the whole year, though only seldom from December to February, without doing any noticeable harm to the vegetation. Plants of the tropical high mountains experience night frosts almost every day and are still adapted to maintain a continuous growth and flowering season. Why then, is it necessary for New Zealand subalpines to develop a definite resting season during the cooler part of the year?

The mild and equable climate west of the Main Divide has probably not required a strong selective adaptation to adverse temperature conditions, but the latter certainly applied during the Pleistocene glacial periods when lower temperatures were more prominent.

Morphology and protective covering of the resting shoot apex is usually viewed in relation to low temperatures and/or drought (e.g. Raunkiaer, 1934). Preliminary studies in this respect by P.Wardle (1963a) show that only a few species possess special mechanisms for bud protection, others are less specialized and some are obviously morphologically unspecialized. As for persistence of leaves during the cool season, only one species (*Hoheria glabrata*) is completely deciduous (at least in the subalpine belt), others are wintergreen, i.e., the old leaves are shed soon after new growth starts; but most are evergreen and may keep their foliage for up to five years or more.

Table 2. Examples for different types of bud coverings (after Raunkiaer, 1934 and Wardle, 1963a).

	resting shoot apex protected by		
young leaves	leaf bases	stipules	scales
Dr.traversii	*Pseudopanax col.*	*Pseudopanax col.*	*Phyllocladus*
Hebe spp.	*Olearia spp.*	*Hoheria spp.*	*Olearia spp.*
	Senecio spp.	*Coprosma pseudo-cuneata*	*Griselinia littoralis*

2. AIMS AND SCOPE OF THE STUDY

The relatively mild and superhumid climate of the New Zealand mountains west of the Main Divide supports a vegetation that may be perceived as an intermediate type between the plant life on wet tropical mountains and the subalpine belt of the northern temperate zone. Though lower temperatures and short days certainly retard plant activity during the cool season, at least certain physiological processes (photosynthesis, metabolism, translocation of nutrients) will continue throughout the year. It was therefore proposed to investigate in what ways New Zealand woody subalpines are adapted to the prevailing climatic regime, with special reference to the nature of the resting period. As most subalpine scrub species seem to survive the common unseasonal frosts without noticeable harm it may be questioned whether the seasonal change in temperature - which does not follow a straightforward trend in some years - or the changing day-length will be more important in controlling the seasonal cycle of plant activity.

An important part of the study was therefore to record and describe the climate of the subalpine belt west of the divide. An attempt could then be made to relate the annual timing of vegetative and reproductive activities to the temperature regime of the particular growing season.

The main emphasis of the study, however, has to be the investigation and description of the ecology of some selected trees and shrubs that are both typical and common of the subalpine forest vegetation in order to get information on their particular life strategies. This would include the investigation of their annual rates of wood increment, shoot growth, leaf area growth; the description of their inherent growth habits (architecture), and modes of vegetative regeneration and sexual reproduction. Animal factors, relevant to flower pollination and predation were also to be given atttention.

In addition, greenhouse trials and laboratory experiments were planned to study germination and growth of seedlings, and to quantify the content of the more important nutrient elements in soil and plant tissue samples.

C H A P T E R II

REVIEW OF THE LITERATURE

Publications on the New Zealand subalpine scrub are scarce and usually limited to describing its floristic composition (e.g. Cockayne, 1899; 1906; 1928). The vegetation is of no commercial value and grows in inaccessible terrain with annual rainfall between 5,000 to more than 10,000mm, so that its scientific investigation has been somewhat neglected. Its role as watershed protection was recognized in the 1950s, as noxious animals (possum, red deer, chamois) were browsing heavily on the scrub. Interest in its ecology has increased recently (e.g. Wardle, 1960; 1961; 1962; 1963a).

As early as 1899 L.Cockayne wrote the first of a series of papers concerned with the regeneration of subalpine scrub at Arthur's Pass after fires had destroyed a good deal of the area's original vegetation. He noted a change in floristic composition with species of *Hebe*, *Dracophyllum longifolium*, *Senecio bennettii* and *Cassinia vauvilliersii* dominating the early second growth scrub. The course of the succession was checked again about thirty years later (Cockayne and Sledge, 1932; Cockayne and Calder, 1932). It was then obvious that the burnt mountain beech forest at the southern end of the pass was being replaced by subalpine scrub. The widespread Hebes of the early stage were by now in decline. In 1969, another paper on the succession at Arthur's Pass was published by J.W.Calder and P.Wardle. The authors noted the decline of *Cassinia* and

recognized a phase of *Senecio bennettii* dominance from about forty to seventy-five years after the fire before the slower growing species of the original scrub take over. Trees of *Dracophyllum traversii, Dacrydium biforme* and *Libocedrus bidwillii* will need at least another hundred years to reach maturity (Calder and Wardle, 1969). These four papers, though still largely descriptive, are the first to deal in detail with secondary succession in the subalpine scrub.

Valuable basic information on the floristics and ecology of subalpine scrub has been provided in a number of articles by P.Wardle. He describes in some detail the subalpine vegetation of the Hokitika catchment (Wardle, 1960) and the Tararua Range (1962), gives an account of growth habits, annual growth rates, leaf persistence and maximum ages for a variety of subalpine trees and shrubs (1963a), and comments briefly on xeromorphic features in humid subalpine environments (1965). Further information (e.g. altitudinal and latitudinal zonation of the New Zealand vegetation) can be obtained from his papers on evolution and distribution of forest vegetation (Wardle, 1963b; 1964), on New Zealand timberlines (1971, 1973), and on detailed local vegetation surveys (Secretary Island, 1963c; Westland National Park, 1977).

There is hardly any information on the autecology of the particular species of the subalpine scrub. The botanical descriptions of the species in the manuals of Hooker (1864), Kirk (1899), Cheeseman (1925), and Allan (1961) include usually two or three lines regarding the distribution and habitat in very general terms; critical information is

often missing. Data on the flowering time of *Dracophyllum traversii* and *Senecio bennettii*, for example, was not available to these authors.

Hoheria glabrata, being not strictly a subalpine tree only, has already been dealt with on several occasions because of its deciduousness; a rare example among the otherwise evergreen woody vegetation (Cockayne, 1900; 1904; 1906; Bussell, 1968a;b). Bussell (1968a) found that leaf fall in *Hoheria* is induced by low temperatures rather than by shortening days and that the growing season is controlled by a change in daylength and temperature and not by short days alone.

P.Wardle (1960) also gives autecological notes on *Hoheria glabrata*, *Olearia ilicifolia* and *Dracophyllum traversii*, in which he states their altitudinal range and site requirements and estimates height growth and average annual increment growth. More detailed information was given in a subsequent study (Wardle, 1963a) when growth habits of a variety of subalpine trees and shrubs were investigated. The data obtained include annual shoot growth, width of growth rings, type of bud protection, etc.

In a joint study investigating the freezing resistence of New Zealand trees and shrubs (Sakai and Wardle, 1978) the experimental temperature limits for freezing injury of leaves, buds, cortex and xylem of *Hoheria glabrata* and *Senecio bennettii*, amongst many others, were reported.

In 1970 J.Wardle and J.Hayward examined the browsing pressure on the forests and scrublands of the upper Taramakau catchment. *Hoheria glabrata* and *Senecio bennettii* were listed in an "extinction" group, i.e., species that will

become only a minor constituent of the vegetation with continuing browsing pressure. *Olearia ilicifolia* and *Dracophyllum traversii* proved to be not particularly influenced by the noxious animals and were classified as browse-tolerant species.

So far, two subalpine woody species, *Phyllocladus alpinus* and *Olearia colensoi*, have been thoroughly treated in the *"Biological Flora of New Zealand"* (P.Wardle, 1969; Wardle, Field and Spain, 1971).

There is a number of other scientific publications that are marginally relevant to the present study. Dunwiddie (1979) took increment cores of *Phyllocladus alpinus* and *Libocedrus bidwillii* at Pegleg Flat, Arthur's Pass, and presented a tree-ring chronology dating back to the early 18th century.

T.Chinn (1975) traced late Quaternary snowlines and cirque moraines in the Waimakariri watershed including the investigation area at Pegleg Flat. He gave exact altitudinal limits for the present snowline which ranges from 1900m on southern aspects to 2120m on N-facing slopes.

A brief comment on the scrub and forest vegetation of Arthur's Pass, particularly the situation of the timberline and wind influence is found in overseas literature (Schweinfurth, 1966).

C H A P T E R III

THE INVESTIGATION AREA

1. THE SELECTION OF THE INVESTIGATION AREA

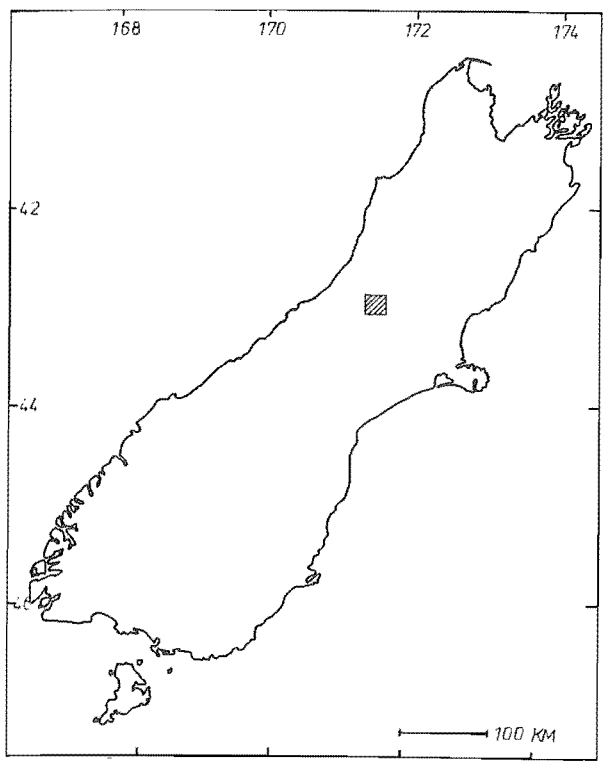

Figure 2. Map of the South Island of New Zealand with location of the investigation area.

When planning and preparing the research on subalpine scrub ecology it was important to choose a location with adequate subalpine vegetation that would be easily accessible under almost any weather conditions because regular serving of the climate stations and frequent growth measurements of the trees was of vital importance for the success of the study. There are, in fact, only two locations in the South Island where roads give access to the subalpine belt of the wet western region. One is the access road to the TV-transmitter at Sewell Peak in the Paparoa Range, the other is the

highest portion of State Highway 73 at Arthur's Pass. As the latter is a good deal closer to Christchurch and only half an hours drive from the Botany Field Station at Cass, which served as a base camp, it was decided to carry out the field studies here, in spite of some shortcomings of this location. Firstly, the status of a National Park imposes certain restrictions on the sites and sizes of sampling procedures. Secondly, the subalpine forest at Pegleg Flat is at the eastern margin of the western subalpine flora and is somewhat isolated by the rugged terrain of the upper Otira gorge. Furthermore, the local mountain climate is

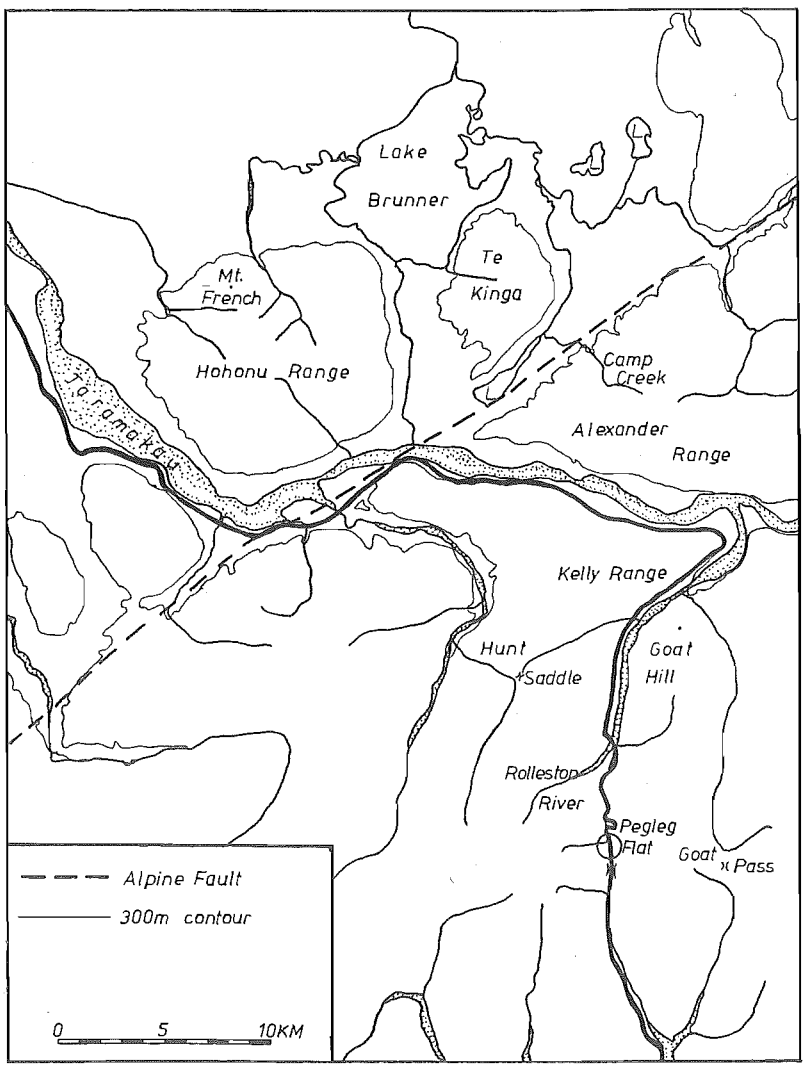

Figure 3. Map of the area N and W of Arthur's Pass, locations mentioned in the text are indicated.

likely to be more "continental" and therefore differs in some aspects from that of the western ranges that are fully exposed to the westerly winds. Finally, an extensive part of the forest and scrub was burnt in the late 19th and early 20th century and today a modified vegetation is present as a result. But this process of vegetation change is well recorded by Cockayne and other authors and could be taken into consideration and even provide useful material for the study.

In order to get a more extensive impression of the vegetation, stands of subalpine forests in the Deception, Rolleston, Otehake, and Kellys Creek catchments were briefly examined as well. Several trips to the western granite ranges around Lake Brunner allowed a comparison of the floristic composition of these mountains with that of the Southern Alps proper.

2. GEOGRAPHY AND LANDFORMS

Arthur's Pass provides the only direct road and rail link between Canterbury and Westland. The Main Divide is crossed at a relatively low lying saddle (922m) that separates the Bealey and Otira catchments. Both rivers run in a N-S direction and join up with the W-E orientated valleys of the Waimakariri and Taramakau. Whereas the Bealey valley lies at an altitude of 800 to 600m for most of its length, the Otira River quickly drops from above 800m at Pegleg Flat to less than 500m at the mouth of the Otira gorge and to about 250m at its confluence with the Taramakau. The valleys were filled with glaciers during the Pleistocene glaciations and the Arthur's Pass saddle itself was repeatedly

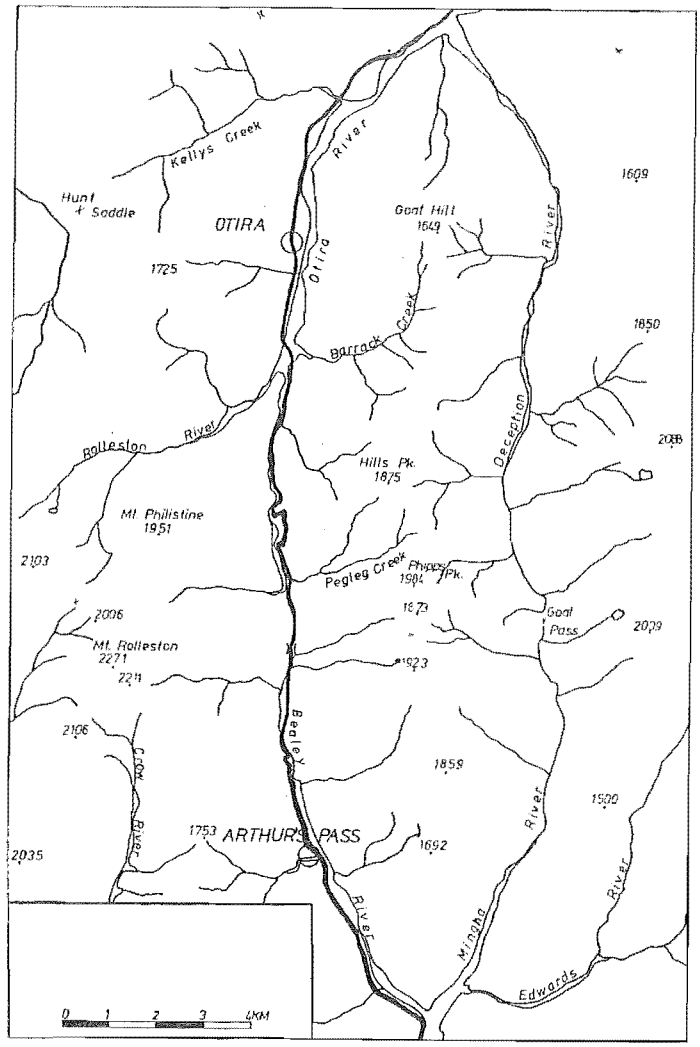

Figure 4. Map of Arthur's Pass area with place names mentioned in the text.

ice-covered during several early Holocene cold periods when the mountain glaciers advanced briefly. The glacial events left their obvious marks. The valley walls are steep and sometimes near vertical and the numerous waterfalls of the smaller tributaries - now draining hanging valleys - indicate the approximate height of the trimline. Above the trimline the slopes are usually considerably less steep and covered in alpine tussock-grassland.

The mountains to the west of the pass rise to over 2000m, Mt.Rolleston (2271m) being the highest peak. These mountains carry New Zealands northernmost glaciers. The tops east of the traverse are slightly below 2000m and not

glaciated at present. Further east, Goat Pass (1076m) lies in a similar position to Arthur's Pass on the Mingha and Deception River watershed (refer to map, figure 4).

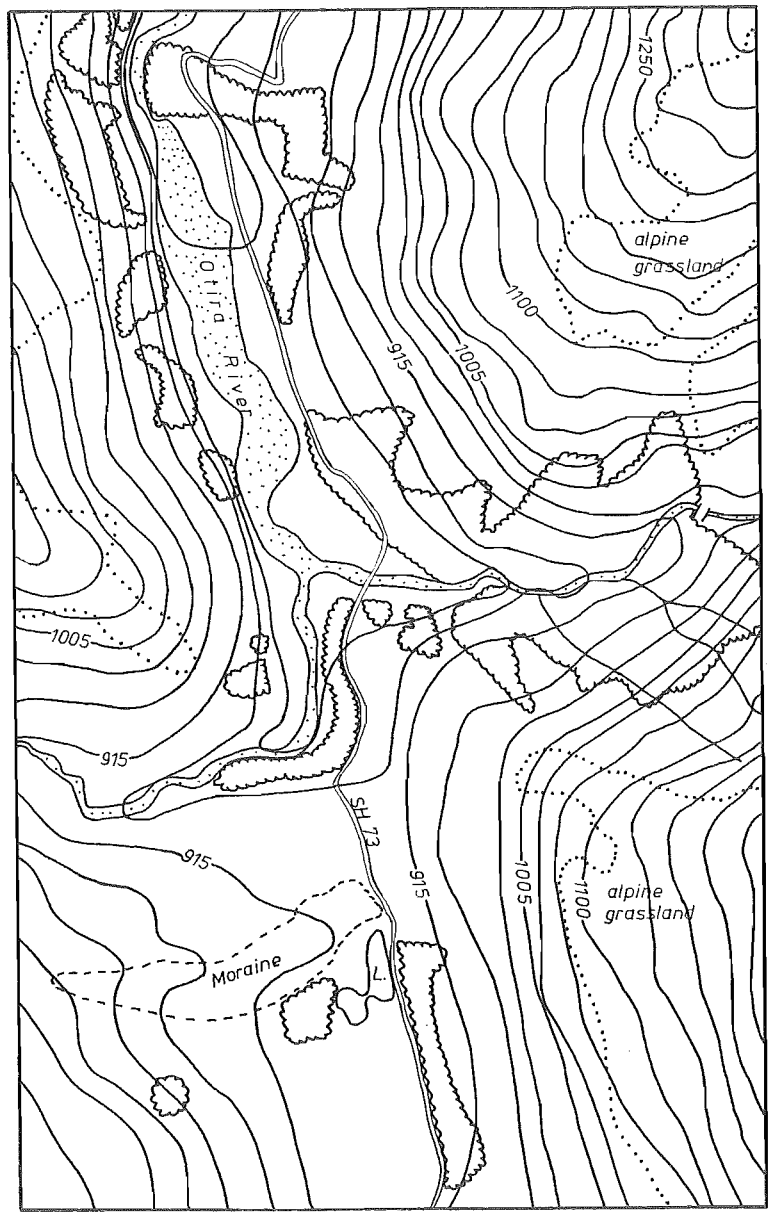

Figure 5. Map of Pegleg Flat outlining the present distribution of subalpine low forest (scale appr. 1 : 11,600).

Pegleg Flat is an about 800m long stretch of flat ground between the Pegleg Creek - Otira confluence and the head of the Otira gorge. The western two thirds of the flat are occupied by the riverbed and several recent shingle

terraces of the Otira River. The remainder is formed by an older terrace (about 830m a.s.l.) that supports grassland and some subalpine scrub. The slopes of Mt.Philistine to the west are very steep cliffs for most of the length of the flat and are clad with scattered scrub and small clumps of subalpine low forest on the talus fans. The eastern slopes - spurs of Hills Peak and Phipps Peak - are quite steep as well but able to support a closed scrub vegetation and stretches of low forest at their lower parts. The gorge of the Pegleg Creek is E-W orientated and its N to NW facing slopes bear the most diverse stands of subalpine scrub and low forest of the investigation area.

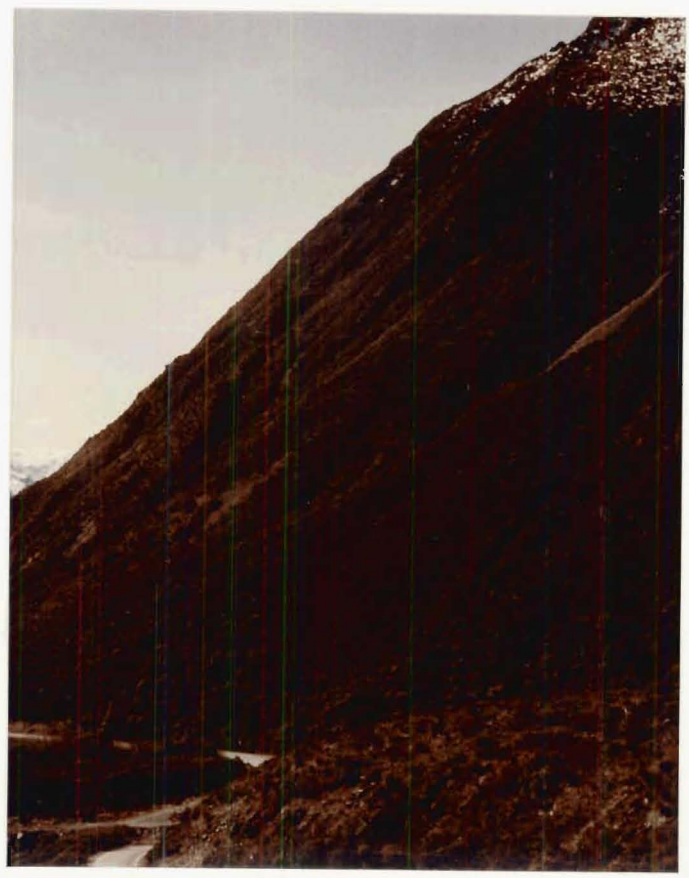

Figure 6. The western slope of Hills Peak with subalpine scrub at its lower part and alpine grasslands above scrubline.

3. GEOLOGY OF THE INVESTIGATION AREA

The bulk of the Southern Alps is composed of rather uniform sedimentary rocks commonly called greywacke. These sediments, of unknown thickness, comprise weakly metamorphosed sandstones, siltstones, and, to a lesser extent, conglomerates of Carboniferous to lower Cretaceous age known as the Torlesse supergroup. The rocks in the vicinity of Arthur's Pass, recently described by Cave (1982), are of Oretian to Warepan time (Upper Triassic). The sediments are shelf and continental slope deposits and are quartzofeldspathic in composition. To the west of Arthur's Pass the sediments of the Torlesse supergroup grade into the more strongly metamorphosed Alpine Schists of the Haast Schist supergroup. These form a 10-20km wide belt, its western boundary is the Alpine Fault.

The sediments were deformed in several successive phases of folding during the Rakaia Orogeny in the early Jurassic. Faulting and uplift from upper Tertiary until Recent formed the Southern Alps and are continuing today. Cave (1982) calculated an uplift rate of 10-11mm/y for the Arthur's Pass area which is in accordance with data from other locations.

The high uplift rates are partly counterbalanced by rapid erosion of the mountains. The greywacke rocks are particularly prone to weathering and subsequent erosion which is accelerated by the local climate. Severe frosts at higher altitudes during the wintertime cause fragmentation of rocks which accumulate in large screes on the slopes. The high rainfall - often in the form of severe rainstorms - causes downslope movements of debris, landslides and rock-

falls; most of the material will be quickly transported downstream by the swollen rivers.

Peaks of erosion occurred during the ice-ages when mountain glaciers advanced during several successive glaciations and deeply carved out U-shaped valleys and steepened the hillsides. Most deposits of the Pleistocene Glaciations have long since been wiped out by erosion processes. Chinn (1975) located ice-contact gravels associated with the late Pleistocene Otira Glaciation only at Arthur's Pass. Holocene glacial events are far better discernible. Moraines and fluvioglacial gravel of the early Holocene McGrath Advance are found in the upper Bealey valley. A close succession of at least three terminal moraines at the top of the pass have been associated with the subsequent Arthur's Pass Advance. The distinct moraine in the upper Otira valley is at least 4000-5000 years old (Burrows, 1978; Cave, 1982) but may be up to 10,000 years old (C.J.Burrows, pers.comm.). Younger advances sometimes left small moraines higher up in the valleys. Since the turn if the century all glaciers have been rapidly retreating leaving only a few small cirque glaciers in the mountains west of the pass.

The uplift of the Southern Alps is accompanied by, at times, violent earthquakes. The last to affect the Arthur's Pass region was the Arthur's Pass earthquake of 9th March, 1929 which reached force 6.9 on the Richter scale (Whitehouse, 1983). The center of maximum intensity was the area ENE of Arthur's Pass to close to Lake Sumner as inferred by Speight (1933) from the extent of slope damage and landslides. The most spectacular is the Falling Mountain landslide. Earlier earthquakes may have caused the big rockfall

at the top of the Otira gorge which has been dated at 2000±90 years BP (Whitehouse, 1983).

4. THE SOILS OF THE INVESTIGATION AREA

The parent materials for all the local soil types are the rocks of the Torlesse group, mainly sandstones and siltstones and to a lesser extent mudstones (argillite) or slightly metamorphized semi-schist (phyllite).

The zonal soils of the investigation area are steepland soils related to the high country podzolized yellow-brown earths and podzols (New Zealand Soil Bureau, 1968). Recent soils from greywacke alluvium are found in various stages of development on the terraces of the Otira River and Pegleg Creek. The flat saddle of Arthur's Pass provided the suitable geomorphology for the development of subalpine gley-soils and in places organic soils. At higher altitudes alpine barrens prevail.

Due to the steepland character of the landscape these soils hardly ever develop in situ. The parent material has usually been transported and re-deposited by glacial ice or running water or by gravitational downslope movements such as rockfalls, avalanches and on screes. The fine materials (silt-size and beyond) are mainly derived from windblown loess, formed by weathering at higher altitudes (Burrows, 1968). Even during the time of soil development downslope movement and mixing of horizons by soil-creep continues and either fresh or weathered material may be deposited on top of a mature soil which can subsequently be recognized as buried A or B-horizons. Furthermore, the complete soil cover may be eroded in places and the formation of a new

topsoil and vegetation cover will then occur over hundreds or thousands of years.

Due to these various processes of disturbance and redeposition, the steepland soils usually possess very thick subsoils which contain material with B and C-horizon characteristics. Stones of all sizes are distributed throughout the complete soil profile. The strong weathering and leaching due to the high rainfall soon removes most of the available nutrients and makes the soil strongly acidic (New Zealand Soil Bureau, 1968). The typical subalpine forest vegetation with podocarps, cedar and epacrids produces a strongly acidic litter that decomposes only very slowly and contributes to leaching and acid soil reaction (New Zealand Soil Bureau, 1968).

The high country podzolized yellow-brown earths of the investigation area are divided into the Otira and Whitcombe sets. Soils of the Otira set (Otira stony loams) occur at altitudes of 150 to 1200m with annual rainfall ranging from 3000-5000mm. The vegetation is broadleaved rainforest to subalpine forest and scrub. The soils of the Whitcombe set (loams and stony loams) occur in the same region but generally at higher altitudes than the Otira soils (900-1500m). The rainfall here is even higher amounting to 2500-7500mm, the vegetation is open subalpine scrub to alpine grassland (New Zealand Soil Bureau, 1968).

All steepland soils are very sensitive to disturbance and once the original vegetation is damaged the topsoil may quickly be removed by erosion, exposing the bedrock to accelerated weathering and steady erosion; recolonisation by plants is only very slow.

5. CLIMATE AND WEATHER

(1) The weather pattern of the South Island

New Zealand is situated in the zone of the southern westerlies. The basic weather pattern is therefore controlled by a continuous progression of anticyclones and intermittent low pressure troughs. The anticyclones pass New Zealand in a ENE-direction, their average track lies over the middle of the North Island in February and between New Zealand and Norfolk Island in September/October (Garnier, 1950). As the air rotates counterclockwise around its center, an approaching anticyclone is accompanied by southerly winds; and N to NW winds are following in its wake when departing from New Zealand. Under the influence of an anticyclone most of the country experiences fine weather with clear skies, light winds, and night frosts in winter. As the anticyclone moves east, northwesterlies gradually set in, bringing cloudy skies and drizzle to the west of the Main Divide. The anticyclone is followed by a trough, i.e., a low pressure belt with a related cold front; the northwesterlies freshen and bring heavy rain to the West Coast and Southern Alps, and when particularly strong, the rain spreads to the eastern high country and later to Canterbury. East of the Main Divide, the northwesterlies - having shed all their moisture at the western slopes - are experienced as strong warm and dry Föhn winds. With the passage of the cold front the wind changes to a southerly direction and brings colder temperatures and further precipitation, usually as snow at higher altitudes. In most cases Westland experiences fine weather during the southerly spell. Sometimes there are strong

winds across the divide from the SW to E directions. With the southerlies decreasing, the next anticyclone moves on to New Zealand and the weather cycle starts again.

(2) The climate at Arthur's Pass

Situated immediately NW of the Main Divide, the investigation area experiences a weather pattern similar to that of Westland. It receives vast amounts of rainfall during westerly weather but a rainshadow effect is noticeable when southerly fronts cross the country. Almost all the precipitation occurs as orographic rainfall caused by the obstacle of the Southern Alps in the path of the moist westerly winds. Precipitation increases with altitude and rainfalls are probably heaviest between 900 and 1200m (Garnier, 1950). The wettest month is October, closely followed by September, November and December, and July is usually the driest month. However, there is a considerable variation in rainfall and monthly falls may exceed 1000mm at any time of the year except for the usually drier winter month (June-August). Though snow may fall at any time of the year at higher altitudes, it is more common from May to September but is only important above 1000m (Coulter,1967). At lower altitudes it melts soon or may lie for about a week at a time. The permanent snowline is situated between 1900 and 2120m depending on aspect (Chinn, 1975).

Regular temperature readings are only available since 1978 for Arthur's Pass village (738m) and since 1973 for the Otira weather station (383m). The records show a mean annual temperature of 7.3^{o}C for Arthur's Pass and 9.9^{o}C for Otira. The coldest month is July and the warmest usually February.

Rainfall has been recorded since 1916 at Arthur's

Pass and since 1905 at Otira, the mean annual precipitation being 3950mm and 5075mm, respectively. The Arthur's Pass station is situated east of the divide and experiences a slight rainshadow effect. As precipitation increases with altitude, the investigation area is expected to receive annual amounts in excess of 5000mm.

Both the westerly and southerly fronts are accompanied by strong and gusty winds, these are particularly marked along the saddle of the pass. Trees can only grow in sheltered places here, and exposed shrubs are windshorn and flagged.

The Bealey - Otira valleys extend more or less in a N-S direction and the solar path is considerably obstructed by the surrounding mountain ranges. The particular aspects of the slopes play an important role in regulating the amount of received sunlight. In midwinter even the more favourable N and W-slopes receive only three and a half hour of sunlight; southern slopes do not receive any direct sunlight at all for several months during the winter.

6. THE SUBALPINE VEGETATION OF ARTHUR'S PASS

When crossing the Main Divide at Arthur's Pass, there is a remarkable change of the vegetation along the route. The increasing diversity of plant life from S to N (which is actually E to W due to the SW-NE orientation of the Southern Alps) is, for the most, caused by the distinct W-E gradient of rainfall and toa lesser extent a result of past glacial events and related vegetation history.

The mountain beech forest of the lower Bealey valley contains a number of broadleaved shrubs in the understorey;

Griselinia littoralis, *Fuchsia excorticata*, *Hoheria glabrata*, several species of *Hebe* and *Pseudopanax*, and a variety of ferns become increasingly abundant - quite unlike the "drier" beech forests south of the Waimakariri. North of the Arthur's Pass settlement, almost all the species of the western sub-alpine scrub and forest are present; *Olearia ilicifolia*, *Senecio bennettii*, *Archeria traversii*, *Dracophyllum traversii* and *Dracophyllum longifolium*, *Pittosporum divaricatum*, *Libocedrus bidwillii*, and many others. But they are still mainly understorey shrubs and trees and overtowered by mountain beech; species like *Libocedrus bidwillii* and *Dracophyllum traversii* are able to make up only a small portion of the canopy.

Figure 7. Southern approach to Arthur's Pass with the timberline of the mountain beech forest in background.

At the saddle the beech forest ceases abruptly at an altitude of less than 900m but ascends to at least 1100m at

the windsheltered southern slopes of Goldney Ridge north of the Bealey River. Schweinfurth (1966) attributed this relatively low lying timberline to increased windspeed at the saddle. There is a small isolated grove of apparently healthy looking beeches shortly north of the Lower and Upper Twin Creek confluence and another outlier of beech forest is found in the gorge of the Upper Twin Creek. The last far advanced group of southern beech is situated due south of the Otira moraine west of Lake Misery. The whole length of the saddle from Upper Twin Creek to Lake Misery is covered with bog and swampy tussock grassland. Only the slopes and the stretches of the Arthur's Pass moraines are covered more or less densely with subalpine scrub dominated *Dracophyllum longifolium;* in wet but well drained places there are groves of *Hoheria glabrata* and *Olearia ilicifolia*.

Figure 8. *Dracophyllum longifolium* scrub on a bouldery moraine at the top of Arthur's Pass.

The first continuous stretch of subalpine forest is restricted to the W-facing slope of Phipps Peak about Lake Misery. This is a low forest dominated by *Hoheria glabrata, Olearia ilicifolia* and *Pseudopanax colensoi,* with *Senecio bennettii* and several species of small-leaved Coprosmas in the shrub-layer. The average canopy height is 3-3.5m, some individuals of *Hoheria* and *Olearia* reaching 4-5m. This forest soon grades into scrub upslope, the estimated tree limit being 940-950m. Most of this forest and scrub seem to have survived the fires earlier this century and possibly the late 19th century fires as well. West of Lake Misery is a small clump of original subalpine forest that also escaped the series of fires (Cockayne, 1899), the main canopy species are *Phyllocladus alpinus,* and *Dracophyllum traversii.* The slopes between the Otira Moraine and the Otira River are only covered with scattered scrub with either *Senecio bennettii* or *Dracophyllum longifolium* being more abundant locally. A waterlogged site NW of the moraine supports only scattered scrub of pink pine (*Dacrydium biforme*) and some *Dracophyllum longifolium.* The N to NW-facing slopes (830-860m altitude) from the bend of the Otira River to the Pegleg Creek gorge provide the most favourable sites and support the most diverse stands of subalpine forest of the investigation area. The main species are *Dracophyllum traversii, Griselinia littoralis, Pseudopanax simplex, Phyllocladus alpinus* and some *Podocarpus hallii,* the canopy height is 4-6m with a scattered overstorey of *Libocedrus bidwillii* up to 8-12m tall. Restricted to these associations on the warmer N-facing slopes are species like *Libocedrus bidwillii, Coprosma foetidissima, Hymenanthera alpina, Pittosporum*

divaricatum, *Pseudopanax simplex*, *Pseudopanax lineare*, and the climbers *Parsonsia capsularis* and *Rubus schmideloides* var. *subpauperatus*.

Figure 9. View of the subalpine low forest at the N slope of Phipps Peak with *Senecio bennettii* scrub above treeline. Note grove of bare *Hoheria glabrata* to the right.

Another type of subalpine forest is found on the river terraces of the Otira River and Pegleg Creek, it consists mainly of *Hoheria glabrata* and *Olearia ilicifolia*, and some *Griselinia littoralis*. *Hoheria glabrata* also forms almost pure stands on old healed slips (figure 9). The forest north of Pegleg Creek - on S to SW-facing slopes - contains only *Phyllocladus alpinus*, *Dracophyllum traversii* and *Griselinia littoralis* as canopy species. The western slopes of Hills Peak support a mixed composite scrub of 3-4m height with *Olearia ilicifolia*, *Senecio bennettii*, *Pseudopanax colensoi*, *Myrsine divaricata* and a number of Coprosmas

Figure 10. Close-up of the subalpine low forest and scrub on the southern bank of Pegleg Creek.

Figure 11. Subalpine low forest dominated by *Olearia ilicifolia* (pale green crowns) on a terrace of Pegleg Creek.

as the main canopy species. *Dracophyllum longifolium* dominates on sites with shallower soils. Further upslope, after the canopy has opened up, *Olearia colensoi* (leatherwood) appears in the scrub. It is only established north of Pegleg Creek and seems to take over the role of *Senecio bennettii* as the major shrub above the treeline.

Scattered individuals of rata (*Metrosideros umbellata*) appear at the cliffs west of the Otira River and in one location on its eastern side at the N-facing wall of a small gorge. After passing the huge rockfall deposit where vegetation is scarce, the rocky slopes support a rata dominated scrub. Rata occurs as a stunted, much branched shrub about three metres tall. Downslope this scrub soon grades into rata-kamahi forest typical of the western side of the Alps.

Figure 12. Tall subalpine scrub dominated by rata (*Metrosideros umbellata*) north of the large rockfall at the northern end of Pegleg Flat.

7. HUMAN IMPACT ON THE VEGETATION OF ARTHUR'S PASS

The transalpine pass across the Bealey - Otira River watershed was known to the Maori but was rarely used (May, 1967). In March, 1864, Arthur Dudley Dobson and his brother Edward explored Arthur's Pass as a road link between the West Coast and Canterbury was urgently required. A track over the pass had been used by a handful of diggers en route to the goldfields after the 1864 gold strike at Greenstone but a peak of the traffic was reached in spring 1865 when more than 1300 men crossed the pass on the dray road then under construction. In February, 1866, this road was finished and connected Christchurch with Hokitika.

It was during these initial years that the vegetation of the pass was severely modified. When the Dobson brothers explored the area they had to hack their way through dense scrub till they reached the swampy flat at the top of the pass. Most of this scrub was later burnt and the flat between the pass and Lake Misery was used as a temporary paddock as about 40,000 sheep and 25,000 cattle were driven over to Westland in the year 1866 alone. For some time Pegleg Flat was the site for the road construction camp. Parts of the subalpine forest here would most probably have been cut down for firewood and the larger trees used for construction. There is still evidence of the felling of some *Libocedrus bidwillii* specimens, the rotting stumps show that the trees were actually cut off and did not die of natural causes.

The greatest impact on the vegetation was experienced during the construction of the Midland Railway line between about 1890 and 1923. A most careful survey had to be carried

out to determine the line of the railway tunnel between Arthur's Pass and Otira. Therefore, all the scrub between the beech forest at the southern end of the pass and Pegleg Creek was deliberately burnt in 1890. Though a previous fire was thought to have occurred in about 1878, the 1890 fire was the most extensive one and only a few fragments of scrub escaped unharmed. A description of the extent and effect of these two fires was given by L.Cockayne in 1899. Part of the beech forest was also cut and burnt in 1906/7 for a further survey for the tunnel line. More scrub fires of lesser extent were noted by Calder and Wardle (1969) as having occurred in 1921, 1930, and 1932.

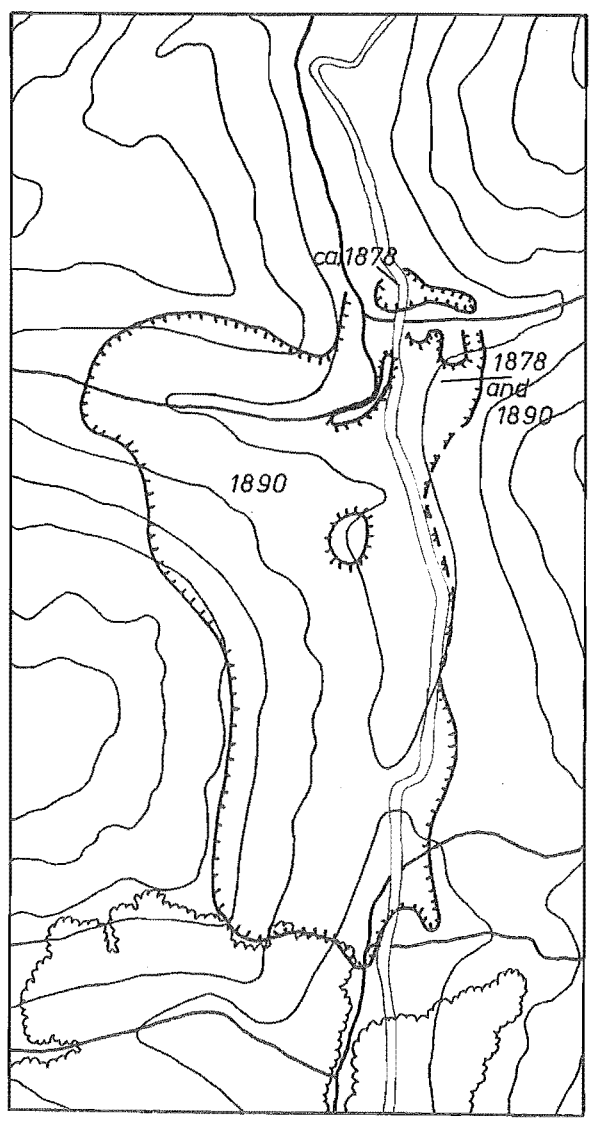

Figure 13. Map of the Arthur's Pass area outlining the minimum extent of the 1890 fire (after description by L.Cockayne, 1899).

Further disturbance, though on a minor scale, was created by the construction of the power pylons over the pass in 1937 and during the sealing of the road between 1963 and 1971. Disturbance by road realignment and mining of gravel for roading during the 1970s also caused some severe local damage.

An indirect result of the human impact is the damage done to the vegetation and landscape by introduced animals. In the Arthur's Pass area only four species are of importance, namely red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), brushtail possum (*Trichosurus vulpecula*), and hare (*Lepus europaeus*). Red deer were first released in the Poulter valley in 1908 and 1909 (Wodzicki, 1950). Wodzicki's distribution map of 1947 states "medium to heavy infestation" of all mountain land from the Whitcombe Pass to the Hope Saddle in the north. But deer do not seem to have played an important part in the upper Bealey and Otira catchments (I.Payton, pers.comm.), traffic noise from the state highway may deter the animals from entering the valley. Deer and chamois were more frequently encountered in the area during the 1940s and 1950s and may have caused local damage to the subalpine scrub (C.J.Burrows, pers.comm.). The most palatable plants of the subalpine forest and scrub, *Pseudopanax colensoi, Pseudopanax simplex, Senecio bennettii, Hoheria glabrata, Griselinia littoralis, Coprosma foetidissima,* and *Coprosma pseudocuneata* are still growing in great abundance in the investigation area.

Chamois was seen only once during the study at an altitude above 1000m in the alpine grasslands at the northern slopes of Phipps Peak. There are, however, a few possums in the area. Their pellets were sometimes found and during the

time of the field work, three carcasses were seen on the road. But so far, no obvious damage to the vegetation has been observed. Hares range widely in the area but their effects on subalpine scrub species are probably negligible.

Wardle and Hayward (1970) reported that the Otira catchment is generally in a far better condition regarding browsing damage than adjacent areas.

8. THE SUBALPINE TREE AND SHRUB SPECIES UNDER INVESTIGATION

(1) The selection of the species

After a preliminary survey on the floristic composition of the subalpine forest and scrub of the area, a few species were to be selected for closer ecological investigation. The species under consideration had to meet the following prerequisites: They should be predominantly denizens of the subalpine belt; they had to be abundant at Arthur's Pass and at the same time should be common in the subalpine scrub of the western side of the Southern Alps. Furthermore, the particular species had to be chosen in such a manner, that a wide range of different ecological habitats of the subalpine belt was covered. Four species met most of the requirements; *Hoheria glabrata* Sprague et Summerhayes (Malvaceae) is the only deciduous tree of the subalpine belt and therefore had to be given special attention. It forms groves on young soils, usually on sites with a history of recent disturbance. These habitats are widespread in the subalpine belt. *Olearia ilicifolia* Hook.f. (Compositae) is generally found on similar sites to *Hoheria glabrata* and is sometimes co-dominant with the former. It was chosen to investigate and compare the strategies of evergreenness

versus deciduousness. *Senecio bennettii* Simpson et Thomson (Compositae) is a tall shrub that is able to thrive on a wide range of different habitats, usually as a constituent of the shrub layer in subalpine forest and especially at forest margins. At Arthur's Pass it is remarkably abundant both above and below timberline. *Dracophyllum traversii* Hook.f. (Epacridaceae) is the only one of the four species that appears to be somewhat restricted to the subalpine and upper montane belt. The species occupies more mature and usually shallow soils, it is gregarious and forms distinct clumps of trees, probably due to the mode of seed dispersal.

(2) Botanical description of the four species

(a) *Hoheria glabrata* Sprague et Summerhayes (Malvaceae). *Hoheria glabrata* (lacebark or mountain ribbonwood) is a small erect tree reaching 10m height; it is deciduous. First order branches are erect or nearly so. The bark of young trees is brown, turning pale in mature individuals. *Hoheria* shows a distinct leaf dimorphism in juvenile versus adult trees. Leaves of small saplings and epicormic shoots of older trees are up to 3x3cm, ovate to suborbicular, cordate and deeply lobed. Normal leaves are 8x4cm to 14x7cm, ovate to broad ovate with the base more or less cordate and tips acuminate, often prolonged into a curved drip-tip. The leaf margins are crenate to dentate. Seedlings and juveniles retain at least part of their foliage during the winter. The flowers are shiny white, to 4cm of diameter and born in small clusters in the leaf axils. The fruit is a slightly compressed sphere, separating into 10-15 compressed, reniform, membranous, one-seeded capsules.

The distribution of *Hoheria glabrata* is lowland to subalpine forest and scrub, it is restricted to the South Island and mainly west of the Main Divide. It is most abundant in the subalpine belt where it occupies river alluvium, talus fans, young slips, and avalanche paths, sometimes in exclusive groves forming the upper timberline. Its maximum age was estimated by Wardle (1963a) as 150 years.

(b) *Olearia ilicifolia* Hook.f. (Compositae). *Olearia ilicifolia* (mountain holly) is a shrub or small tree with a flattened crown (umbrella shaped) sometimes reaching 7-8m in height. The pale brown bark may hang down in long ribbons. The leaves are 5-8 x 1-2cm, linear-oblong, acute to acuminate with a truncate base, coriaceous, glabrous above and with a yellowish white tomentum below. The margins are strongly undulate, dentate with almost spinous teeth. The flowers are white, about 40-60 capitula in corymbs with 10-20 florets each. The seed is a 2mm long conspicuously ribbed achene. The maximum age is 200 years (Wardle, 1963a).

The habitat of *Olearia ilicifolia* is lowland to subalpine scrub with a distribution from latitude 38^{o} to Stewart Island. The species grows on river terraces, fans, talus and slips, often sharing dominance with *Hoheria glabrata*.

(c) *Senecio bennettii* Simpson et Thomson (Compositae). *Senecio bennettii* is a shrub up to 3m tall with grooved branches and yellow-brown papery bark. The leaves are 5-10 x 3-5cm, ovate, sometimes elliptic, glabrous and shining above, clad in appressed silvery white tomentum below. Flower panicles with 30-60 capitula containing 10-25 florets each; the achenes are 2.5-3mm long and ribbed.

Senecio bennettii occurs in lowland to subalpine

scrub from latitude 40°30' (Tararuas) southwards to Stewart Island, but is more common to the west of the Main Divide.

(d) *Dracophyllum traversii* Hook.f. (Epacridaceae).

Dracophyllum traversii (Nei-nei) is a small tree up to 10m or more, the trunk reaching 60cm in diameter. The bark is smooth light brown but often appearing almost black (because of a cover of sooty mould). The leaves are arranged in terminal tufts at the tip of the branchlets, they are 40-60cm long with a 2-3cm sheath, 4-5cm broad above the sheath and gradually tapering into a long filiform tip; the margins are minutely serrulate. The flowers are small, reddish brown and born in stout terminal panicles. The seeds are light brown and tiny.

Dracophyllum traversii is restricted to the South Island from latitude 41° to 43° on the western side of the Main Divide. Its habitat is upper montane to subalpine forest and scrub on well drained sites with moderately leached soils. Wardle estimated a maximum age of 400 years (Wardle, 1963a).

(3) Definitions of the terms "tree - shrub" and "forest - scrub"

In this study the terms tree and shrub will be used following the suggestions of Mueller-Dombois and Ellenberg (1974), i.e., with the major emphasis on the typical growth habit; separation into single trunk and crown in trees and regular low branching near the base of the stem in shrubs. Of course shrubs are generally of lower stature than trees and an arbitrary limit was set at 5m height (Mueller-Dombois and Ellenberg, 1974), though the terms "giant shrubs" (>5m), "small trees" (2-5m), and "dwarf trees" (<2m) have been pro-

posed as well.

Employing this scheme, *Senecio bennettii* will always be described as a shrub, *Hoheria glabrata* and *Dracophyllum traversii* usually as trees unless their growth is severely stunted and does not reveal the typical growth habit. The classification of *Olearia ilicifolia* presents a problem as this species shows a variety of growth habits. Specimens with a single unbranched trunk and branches above 2m height appear as typical trees but low branched individuals between 4-6m height - that should be termed giant shrubs - are mentioned as trees as well during this study.

A similar division has been used for the terms "forest" and "scrub". Mueller-Dombois and Ellenberg (1974) defined scrub as being of 0.5-5m height; taller vegetation is termed forest. The forests at Pegleg Flat attain only a mean canopy height of 5-8m and are described as subalpine low forest. Vegetation of lower stature is called scrub; if it is generally lower than 2m it is referred to as low scrub.

C H A P T E R IV

INVESTIGATION OF THE LOCAL SOILS

1. RECORDING OF SOIL PROFILES AND SAMPLING PROCEDURES

Seven soil pits of about 50 x 30cm dimension were dug, the depth usually being limited by increasing stoniness between 50 and 80cm. One of the faces of the sample pit was then cleaned and photographed. The profile was now sampled at 10cm intervals and an additional sample of the organic horizon was taken as well. These soil samples were intended for the determination of pH and chemical analysis, the weight of individual samples varied from 500 to 2000g. The samples were air-dried and ground to pass a 2mm sieve. The weight of the fractions < 2mm and 2-63mm was determined and calculated on a percentage basis in order to estimate the stoniness of the soils. Stones larger than 63mm were discarded at the sampling site.

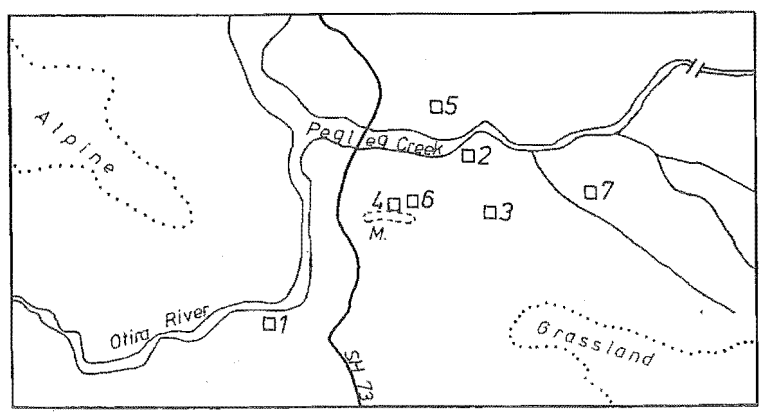

Figure 14. Map of the lower Pegleg Creek catchment with location of the seven sample pits.

2. THE SOIL PROFILES

(1) The texture of the soils.

All sampled soil profiles may be described as very stony or very gravelly, i.e., more than 30% of the weight is made up by the fractions larger than 2mm (Taylor and Pohlen, 1962). Only profile 7 and the upper part of profile 6 may contain less than 30% by weight stones and/or gravel and would be termed stony (or gravelly). Profile 1 is two-layered, the top 25cm is very gravelly the lower part very bouldery; profile 4 is very bouldery throughout (both were estimated to contain 80-95% by weight boulders).

All soil samples taken were also divided into the fractions < 2mm (fine soil for further analysis) and 2-63cm (gravel), and both fractions were weighed. In most cases the fine soil made up 40-60% of these two fractions, only in the upper layers of profiles 5,6,7 the fine soil increased to 70 to over 80% of the weight. These profiles also had the highest estimated clay content indicating a relatively long period of soil formation. Profile 1 had only 12-15%, in one sample 30% fine soil (of the fraction <63mm). Profile 4 showed two maxima for the texture analysis, the first being boulders, mostly in the 30-50cm range but larger ones were also present, smaller stones were relatively rare. The material <63mm consisted mainly of fine sand and silt. The fine sand could have been deposited primarily but may as well be windblown sand trapped in the spaces between the boulders most of which are not yet filled with sediment.

(2) Soil profile development.

With the exception of site 1 which has only developed

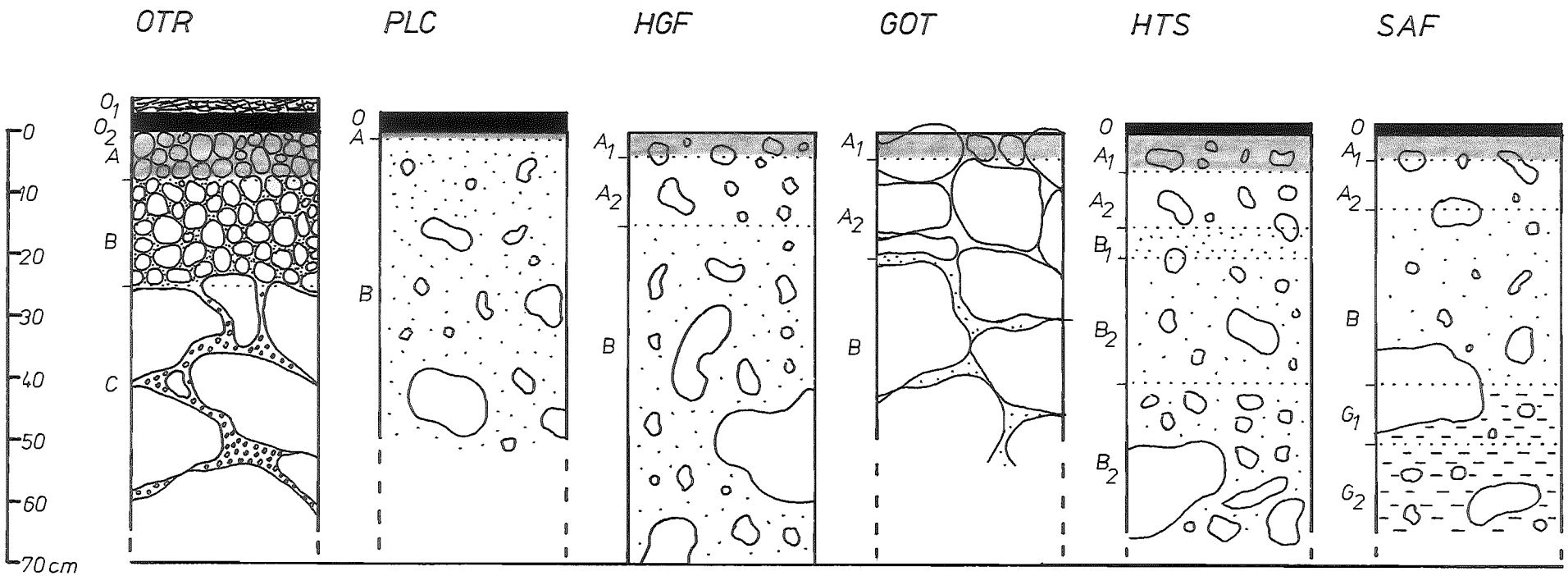

Figure 15. Sketch of the investigated soil profiles showing horizon development and texture (profile 7 (DTC) has been excluded).

a soil in the uppermost 25cm of the profile, all other sites reveal deeply weathered soils to the maximum depth of the pits (50-70cm). Recent slips in the vicinity show that most profiles will be 1-2m deep before reaching bedrock. O-horizons are thin and often discontinuous; only loose *Draco-phyllum traversii* litter may surpass a depth of several centimetres. The profiles 3-6 all have A-horizons of 4-6cm thickness; only profile 7, presumed to be the oldest, has an 8cm A-horizon. The 8cm deep A-horizon of profile 1 seems out of proportion with regard to the recent age of the soil but all organic material has actually been accumulated in the spaces between the pebbles thus penetrating to a considerable depth into the solum.

Profiles 3-7 show obvious indications of A_2-horizons caused by strong leaching (pale colour, lowest pH-value of the profile). The leached horizon reaches down to a soil depth of 15cm and in profiles 4 and 7, i.e., the oldest ones, to 20cm. The remaining lower parts of the profiles have usually been designed as B-horizons, only in profile 6 are there indications of restricted drainage causing a pale yellow to pale grey discolouration. This soil pit, after filling with rain water, never drained again even after dry spells.

3. THE CHRONOSEQUENCE OF THE SOIL PROFILES

(1) The concept of soil chronosequences (Jenny, 1941; Stevens and Walker, 1970).

In related soils certain properties show a directional change along a soil series that is a function of the time which has elapsed since their formation. Such properties

include decrease in pH, loss of original phosphate content, increasing breakdown of mineral particles into successively smaller particle size and degree of chemical weathering, etc. Stevens and Walker (1970) defined a soil chronosequence as

> "A sequence of soils developed on similar parent materials and relief under the influence of constant or ineffectively varying climate and biotic factors, whose differences can thus be mainly ascribed to the lapse of time since the initiation of soil formation."

However, it is difficult to satisfy these requirements perfectly, in particular the dating of a surface will be a problem unless its development was recorded in historical times.

Most soil chronosequences have been studied on soils on glacial deposits and sand dunes, but the surfaces of a system of river terraces provided a suitable subject for the present study. These surfaces can be placed in a relative age sequence and the kinds of substrates and the history of the sites are sufficiently similar to regard them as an age series although not conforming strictly to all the desirable conditions for a chronosequence.

(2) Origin of the terrace system at Pegleg Flat

In most mountain streams the steep gradient and erosive force of the running water causes an accelerated sediment transport downstream and will not allow accumulation of sediment and the build-up of terraces in the upper reaches of the catchments. In the case of Pegleg Flat, however, it appears that the large rockfall at the northern end of the flat blocked the flow of the Otira River. The drainage of the Otira-Pegleg Creek catchments was thus ponded for at least

some time before the present gorge was cut into the talus. It is supposed that at least some of the older terraces were formed during this time of partial blocking of the Otira River which would have resulted in the accumulation of huge quantities of alluvium. Whitehouse (1983) gives a radiocarbon date of 2000±90 years for the rockfall and actually mentions the existence of a former lake.

(3) Description of the geomorphic situation of the soil profiles.

The seven investigated soil profiles were tentatively arranged on a relative time scale on the basis of soil profile and vegetation development. This seemed permissible as profile development is directly related to soil fertility, which in turn, has an important bearing on the present type of vegetation. On the other hand, the relative position of the alluvial terrace surfaces on which the soils developed can also be used as a means of relative dating. Both approaches were employed and gave usually, but not in all cases, coinciding results. In some instances textural differences, and in one instance a past fire, were more important with regard to soil profile and vegetation development than was the relative age of the surface.

As all the bottom and most of the lower slopes of Pegleg Flat are covered by alluvium the superposition of the successive deposits one above another allows them to be dated relatively (see figure 16).

The site 4 (GOT) is the highest of all alluvial sites. Believed to be a fluvioglacial terrace, as indicated by a low terminal moraine and several dead-ice hollows, this

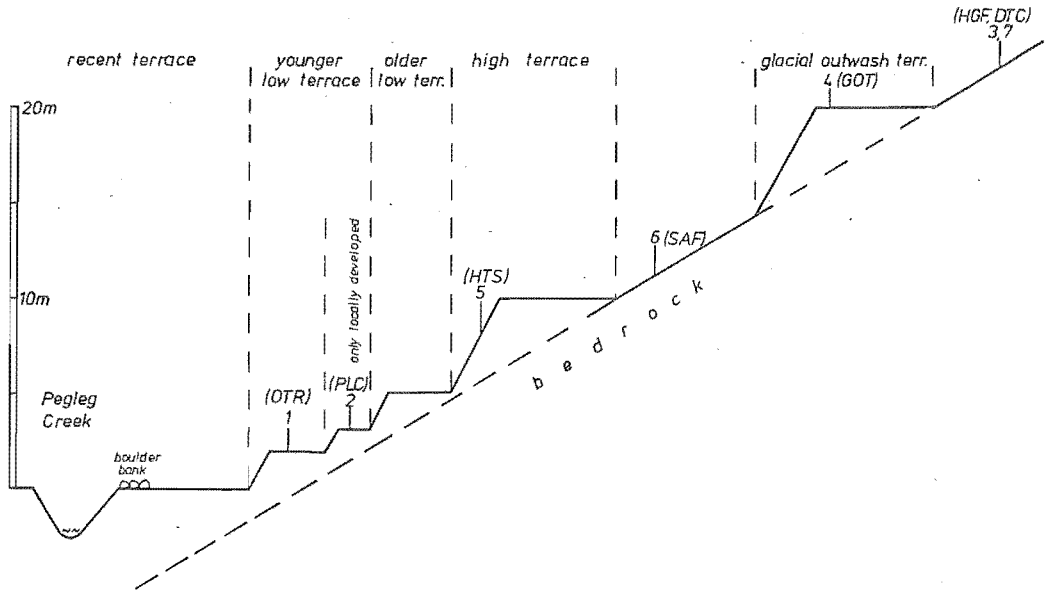

Figure 16. Schematic profile of the terrace systems of the Otira River and Pegleg Creek catchments, the locations of the soil pits are indicated.

deposit is situated at an altitude of about 860m, i.e., at a lower level than the prominent moraine arc of the former Otira Glacier that has been tentatively dated between 10,000 and 5,000 years BP (Burrows, 1978). The fluvioglacial terrace is therefore presumed to be younger than that. The following lower level consists of an old high terrace of Pegleg Creek, remnants of which can be found at both sides of the creek at about 845m. Profile 5 (HTS) is situated at the slope of this terrace system. Older lower terraces are partly preserved at Pegleg Creek and the Otira River. The soil pit 2 (PLC) was dug on one of these remnants, but this site could have received additional talus from the adjacent slope as well. Pit 1 (OTR) is believed to be the youngest profile as shown by the unweathered shingle deposits in its lower part. A minimum age of about 200 years is indicated by the vegetation. *Olearia ilicifolia* trees were cored and

found to be about 180-240 years old. Several overmature and partly fallen *Phyllocladus alpinus*, all of them with multiple stems and presumed to be remnants of the initial occupants of the site, are probably of the same age. Wardle,(1969) citing D.B.Lawrence, gives an age of 190 years or more for this species.

The remaining soil profiles are situated at altitudes above the level of the late Holocene terrace systems. Ages for these soils are hard to estimate as successive erosion and downslope soil creep will have continuously mixed the soil horizons. Profile 6 (SAF) is situated between the fluvioglacial terrace and the older high terrace and very close to the edge of the former. Its deposits may have originally covered the SAF site but were later eroded again. Sites 3 (HGF) and 7 (DTC) are at an altitude of about 900m, i.e., above the level of Holocene glaciations but have different histories. Site 3 is situated in a broad depression in the slope of Phipps Peak, probably caused by a big slip. The fact that there is no superficial drainage system indicates that its bottom is filled with loose talus allowing free subsurface draining. At the lower end of this depression the slope drops steeply towards the Pegleg Creek gorge and any talus has long since been cleared away by the creek. This geomorphic landform is tentatively dated as having been formed between the deposition of the high terrace and older low terrace but may be older still. Site 7 is located on a ridge and may have been influenced by downslope movements of the soil cover.

The ordination originally based on vegetation cover only, is also valid as a soil chronosequence if site 3 is

included as suggested above. Profile 4 which may actually be the second oldest site, does not fill well into the ordination, however; it is covered with open *Senecio bennettii* scrub after being burnt in the late 19th century, but some remnants of the original vegetation clearly show that this site did not support subalpine low forest anyway. This may be deduced because of the nature of the substrate - very bouldery texture with hardly any fine soil - and because of the exposure of the site to the strong winds, preventing the emergence of trees above the shrub layer.

4. SOIL CHEMICAL ANALYSES

(1) Soil chemical methods

(a) Soil pH. The pH values of the samples were determined employing the saturated soil paste method. 25g of air-dried fine soil were weighed into a beaker and distilled water added whilst stirring with a spatula until the required consistency was obtained. The mixture was allowed to stand for one hour. The pH was then measured electrometrically with a glass electrode. The mean of three repeated measurements was listed as the actual pH value.

(b) Soil phosphorus. Total, organic and inorganic phosphorus (as extracted with 1N H_2SO_4) of the soil samples was determined by the "ignition" method described by Saunders and Williams (1955), but 1N H_2SO_4 was used as the extracting agent following the method of Shah et al (1968).

Two replicates of 1g of air dried fine soil were weighed into crucibles and ignited at 550°C for 1h to destroy organic matter and release organic phosphorus. The sample was trans-

ferred into an Erlenmeyer flask, 50ml 1N H_2SO_4 added and, after being sealed with a rubber stopper, shaken on a shaker for 4h. After filtering (Whatman No. 42) 0.2, 0.5 or 1.0ml of the extract was transferred into a test tube and diluted with 3.0 to 3.8ml of distilled water. In the blank and standards the sample solution has to be substituted by the same volume of 1N H_2SO_4.

For colorimetric determination of P, 1ml of a mixture containing sulphuric acid, ammonium molybdate and ascorbic acid was added (Chen, Toribara and Jackson, 1956). The test tubes were placed in a waterbath at 37°C for 90min before the P-concentration was measured colometrically at 820nm with a Bausch&Lomb Spectronic 20 spectrophotometer.

Another, but unignited 1g sample (2 replicates) was treated with the same procedure for the estimation of inorganic P, i.e., acid-extractable and non-occluded P (Shah et al, 1968).

(c) Soil nitrogen. Total soil nitrogen was determined by the microkjeldahl method (lab sheet for Botany stage II, Ecology course, 1977). 0.5g of air dried mineral soil or 1.0g of organic horizon was weighed into a Kjeldahl flask and 5ml of concentrated H_2SO_4 containing 2% salicylic acid were added. The flasks were allowed to stand for 30min but were shaken several times in between. After adding 1g of sodium thiosulphate the mixture was gently warmed for 5min and after adding 2g of potassium sulphate and 0.1g of copper sulphate the heat was gradually increased to full. When the solution cleared pale green heating was still continued for another 15min. After cooling the digest was transferred to a measuring cylinder and diluted to 25ml. An aliquot of 5ml

was transferred to a Markham still, the remaining acid was neutralized with 40% NaOH and steam was allowed to enter the distillation jacket. The condensate was collected in 10ml 2% boric acid solution with a few drops of mixed indicator added. The boric acid solution was then titrated with 0.01N HCl and the amount of nitrogen in the original sample calculated from the concentration of four replicates.

(d) Determination of exchangeable K, Ca, and P by sodium acetate extraction. 10g of air dry mineral soil (5g for organic horizons) were weighed into a 100ml Erlenmeyer flask and 50ml of 1N acetate solution added (68.0g $NaCH_3COO \times 3H_2O$ plus 28.6ml glacial acetic acid per litre). The flasks were sealed with rubber stoppers and shaken on a mechanical shaker for 30min. After the extracts were filtered (Whatman No.42 paper) K and Ca were determined directly on an EEL flame photometer. For P-determination, 4ml of extract (or less for high P-concentrations) were transferred into colorimeter tubes and 4ml of P-reagent added. P was determined as before with a Bausch&Lomb Spectronic 20 spectrophotometer.

(2) Results of the soil pH determinations

The full range of pH values determined for the soil samples was 2.9 to 5.3; most samples were extremely acidic (pH < 4.5), the remainder strongly acidic (pH 4.5 - 5.2) and only one mineral horizon with a pH of 5.3 could be termed moderately acidic (classification after Taylor and Pohlen, 1962). The organic horizons usually have slightly higher pH values than the underlying mineral soil. The striking difference between the pH values of the O-horizons of sites 1 and 2 (pH 5.3) and sites 6 and 7 (pH 3.4, 3.5) is caused

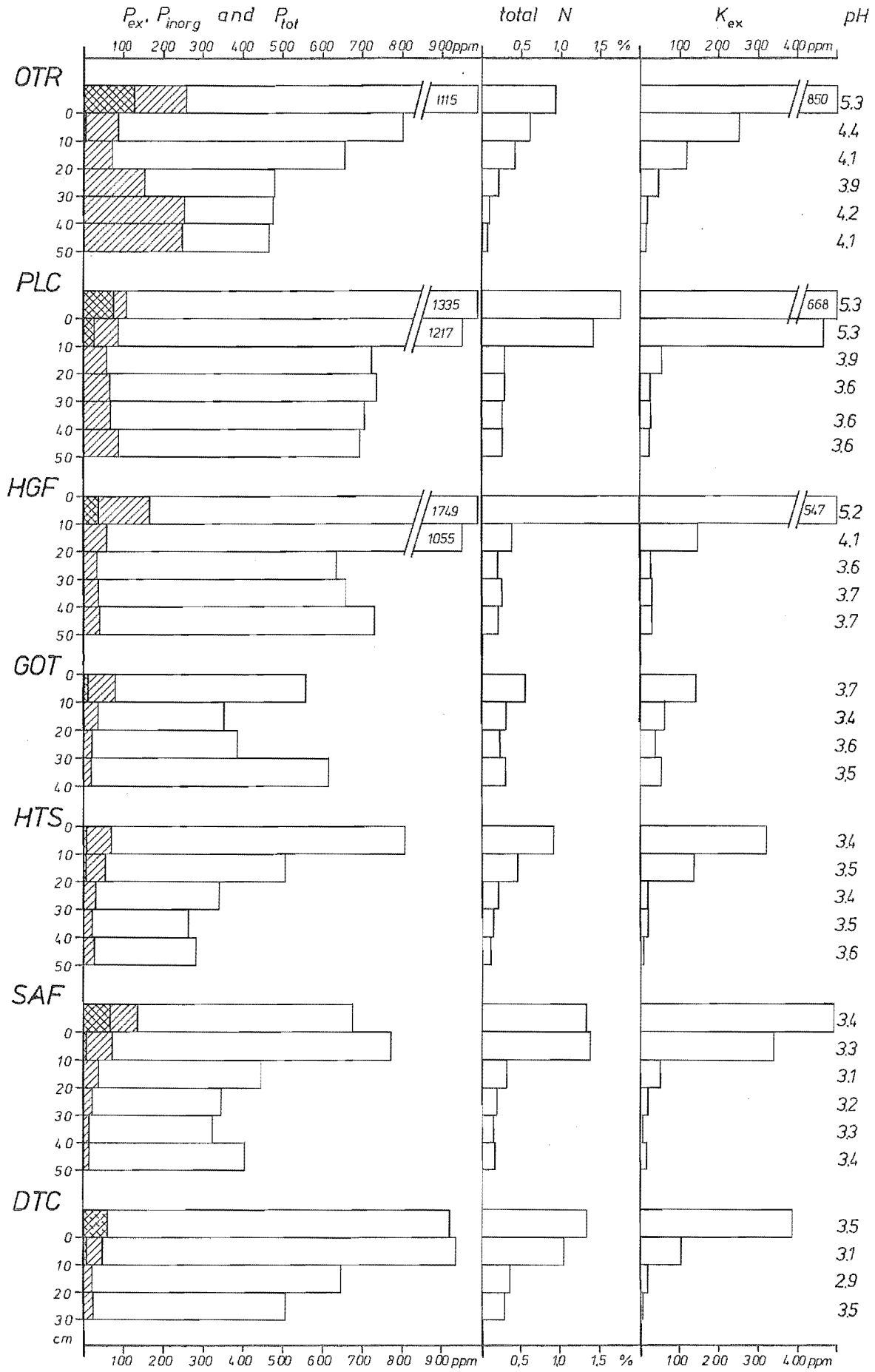

Figure 17. Results of the soil chemical analyses.

by the higher base content of the specific litter (*Hoheria/Olearia* versus *Dracophyllum/Libocedrus*) and the much slower breakdown of the latter.

At site 3 litter decomposition (mainly *Hoheria*) is so fast that it does not accumulate to form a distinct O-horizon; no sample could be taken in this instance, but the A_1-sample with a pH of 5.2 indicates that an O-horizon would tend to show a similar value. The comparatively somewhat reduced pH value of the A-horizon of site 1 (pH 4.4) may indicate the early stage of soil development and is still close to the pH of the C-horizon. The A_1-horizons of site 2 and 3 show maximum values (pH 5.3, 5.2). Site 4 which should be regarded as the second oldest profile has the highest pH (3.7) of the remaining four sites. This could be caused by the different nature of the parent material or texture, but more probably, the ashes of the 1890 fire that almost totally burnt the original vegetation added a fresh base supply to the topsoil that has not been completely leached again since. The pH values of the A_1-horizons for profiles 5,6, and 7 show a declining trend (pH 3.4, 3.3, 3.1) in accordance with the presumed ages of the soils.

The lowest pH value in profile 1 (pH 3.9) coincides with the depth of the soil development, the C-horizon still retains a slightly higher pH. Site 2 has pH values of 3.9 at 10-20cm depth and 3.6 throughout the remaining lower part of the profile. The other five soils have developed A_2-horizons that reveal in most cases the lowest pH value of the entire profile (3.4 in 4, 3.1 in 6, 2.9 in 7). There is not much variation in profile 5.

The bottom samples of nearly all profiles show very

similar pH values ranging from 3.7 to 3.4, only profile 1 has a slightly higher pH of 4.1 owing to the relatively unweathered parent rock.

The lowest pH value of each profile - usually associated with the A_2-horizon - is a good indication of the state of leaching and thus relative maturity of the particular soil. These minimum values show a steady decline along the presumed time scale from pH 3.9 (profile 1), 3.6 (2,3), 3.4 (4,5), 3.1 (6), and 2.9 (7), only profile 4 is slightly out of place because of the already mentioned disturbance by a relatively recent fire.

(3) Total soil nitrogen

Nitrogen is one of the plant nutrients that is usually not present in the parent material before soil formation but must be accumulated in the system by uptake from atmospheric sources, free living or symbiotic N-fixing organisms. It is then recycled by microbial breakdown of plant debris. In the initial stages of soil development - unless substantial amounts of old plant debris are incorporated into the substrate - only plants with low N-requirements or species associated with symbiotic bacteria or bluegreen algae can occupy the new substrate. Once N is locked up in plant tissues, the nutrient status of the soil (with regard to nitrogen) will depend on the rate of breakdown and recycling of N-containing substances. This depends on microbial activity which is influenced by the soil pH. Low pH values tend to suppress N-mineralisation as do low temperatures and initially low N-contents of acid plant litter (high C/N-ratio), especially of mor-forming plants. Thus highest N-contents

should be expected in moderately developed soils. This holds in general for the seven investigated soil profiles. N-contents of the A-horizons are highest (2.0%) in profile 3 under *Hoheria glabrata* forest, declining towards the younger sites (1.4% in profile 2 and 0.6% in profile 1) as well as towards the older soils (1.4% in 6, 1.1% in 7). Sites 4 and 5 have lower values than should be expected, in site 4 (0.55%) the cause is likely to be losses due to the 1890 fire, and the somewhat open vegetation cover as compared with closed subalpine forest in all the other locations. At site 5 (0.9%) lower temperatures could be responsible for the low N-concentrations. This site is situated at the slope of Hills Peak and the solar path is obstructed for some time during the morning in summer and for the whole day during the winter months. This has also affected the floristic composition of the forest here in which several species including *Libocedrus*, *Pseudopanax simplex*, *Pseudopanax lineare*, *Podocarpus hallii*, and *Coprosma foetidissima* are absent. A simple source of error may be natural variation of the N-content and lack of replicated sampling.

Throughout the lower parts of all profiles, N-values are all within the range of 0.1-0.4%, steadily declining with increasing profile depth. The comparatively high N-content of 0.4% in the 10-20cm sample of site 1 indicates that organic matter was easily incorporated into the middle parts of the profile due to the porous nature of the parent material (pebbles). The low values of 0.08% and 0.06% in the 30-40cm and 40-50cm samples show the short time of soil development since the deposit of the substrate.

(4) Soil phosphorus

As opposed to nitrogen, the phosphorus supply of the soil is mainly derived from the initial P-content of the parent material. In the case of the Southern Alps where "greywacke" comprises almost all of the parent rocks, the original P-content is known to be relatively low (Stevens, 1968). Compared with the total soil-N which is expressed on a percentage basis, amounts of total P in the soil are much lower (probably not exceeding 0.2%) and are usually given in parts per million (ppm).

(a) Total phosphorus. Total P was found within the range of 260-1750ppm. P-contents of the organic layers are about 50% higher at the sites 1 and 2 than in profiles 6 and 7. P-reserves of the A_1-horizons are highest for profile 3 (1749ppm) followed by site 2 (1217ppm). About equal values around 800ppm were encountered for the sites 1 and 5-7; site 4, with 555ppm, is the least fertile one. P-contents generally decline with profile depth. The relatively unweathered material in the lower profile of site 1 contains about 465-480ppm P, giving an idea of the original P-content of the parent rock. This value is surpassed in the comparable profile depths of site 2 and 3 (630-730ppm), and for some reason in the 30-40cm sample of profile 4, but lower values (260-400ppm) are encountered in profile 4 (20-30cm sample only), profiles 5 and 6, and most probably in profile 7 (this profile ends at 30cm depth showing 506ppm P).

(b) Inorganic phosphorus. The fraction termed inorganic P also includes all exchangeable P that is extracted by the strong solvent 1N H_2SO_4. This is particularly obvious in the O and A-horizons where high P_{inorg} values are, for the

most part, due to phosphate ions adsorbed to humus particles. Part of the P_{inorg} is phosphate from organic material that is released after mineralisation and now enclosed in the so called secondary minerals like Fe and Al-phosphates. Primary P-minerals, like apatite ($Ca_3(PO_4)_2OH/F$), occur only in the parent rock and are soon released by weathering processes.

The mentioned primary P-minerals are supposedly present in profile 1 only where values for P_{inorg} increase with depth to 250ppm in the unweathered lower part. Possibly, the slightly higher values of P_{inorg} at the bottom of profile 2 are also partly made up by primary P-minerals. When expressed as a percentage of P_{tot}, which decreases with profile depth, the P_{inorg} values of these two profiles reveal a more obvious rise down the profiles. P_{inorg} contents in the remainder of the profiles are supposed to be made up by Al and Fe-phosphates and exchangeable adsorbed phosphates. Most A_1-horizons contain between 70 and 90ppm inorganic P, profile 7, the most severely leached one, contains only 50ppm. In profile 3 the high value of 160ppm reveals the relatively fast mineralisation of the *Hoheria* litter. Throughout the middle and lower parts of the profiles 3-7, P_{inorg} values range from 20-40ppm P, decreasing to around 10ppm at the bottom of profile 6 and most probably profile 7.

(c) Exchangeable phosphorus. The fraction P_{ex} comprises all phosphate ions in the soil solution and part of the adsorbed P that is more or less firmly fixed to organic matter or clay minerals. P_{ex} values are therefore usually correlated with organic matter content in the O and A-horizons.

P_{ex} values of the O-horizons are highest in profile 1

(129ppm) followed by profile 2,6, and 7 (76, 67, 60ppm). Values for the A_1-horizons are 37.5ppm for profile 3, 23.5 ppm for profile 2 and range from 9.5-7.0ppm in profiles 4,6, and 7. Profile 5 has, with only 4.6ppm, a lower value than would be expected. The lowest value of 2.2ppm in profile 1 is due to the early stage of soil development with comparatively little organic matter and clay particles in the topsoil resulting in a low exchange capacity.

The P_{ex} values in the lower parts of the profiles are, with the exception of two samples, smaller than 1ppm, usually declining with depth. Mean values would be 0.9ppm (10-20cm), 0.5ppm (20-30cm), 0.2ppm (30-40cm), and a slight increase to 0.45ppm at 40-50cm depth.

(5) Exchangeable potassium

Potassium occurs extensively in igneous rocks and related sedimentary rocks mainly as a component of the feldspars and other silicates. It is released by chemical weathering but most of it is again fixed in the various clay minerals that form as secondary minerals in the process of weathering. The content of exchangeable soil potassium is therefore in close relationship with clay formation which in itself is a measure of soil development. Potassium should become more and more available as a plant nutrient with increasing weathering of the soil, but at a later stage, after K-supply from the weathering of the primary minerals has been exhausted and especially after the clay minerals have been removed from the topsoil by illuviation, K_{ex} values will rapidly decline again and the only available potassium may be the K-ions released by decomposition of organic matter.

The highest K_{ex} values were found in the O-horizons

ranging from 850ppm in profile 1 and 668ppm in profile 2 to 495ppm in profile 6 and 387ppm in profile 7. The K_{ex} values of the A_1-horizons were on the average considerably lower but very closely related to the presumed age of the soils. Starting with 250ppm in profile 1, K_{ex} values rise to 465ppm (2) and 547ppm (3), than decline again to 320ppm and 341ppm (profiles 5,6), and to only 140ppm (4) and 103ppm in profile 7. The controversial profile 4 is for the first time represented in its right position on the presumed relative time scale of soil development. There is only a minor difference between the K_{ex} values of profile 5 and 6.

In the subsequent 10-20cm layers, profile 3 has, with 145ppm, still the highest and profile 7, with only 19ppm, still the lowest value but in the other 5 profiles no apparent trend is revealed. In the bottom layer (30-40cm and 40-50cm), profile 1 has about 15ppm exchangeable potassium, profile 2 and 3 20-30ppm, and profiles 5,6,7, with 10-20ppm, the lowest values of all. Profile 4 still holds 55ppm at 30-40cm depth, possibly as a result of the 1890 fire.

(6) Exchangeable calcium

Calcium is present in primary minerals like feldspars but it is more widespread as the calcium carbonate of sedimentary rocks. As the Torlesse rocks (greywacke) of the Southern Alps consist almost entirely of sandstones, siltstones and mudstones, the calcium content of the parent rocks can be expected to be very low. Also, high rainfall and low pH values of most soils would lead to fast leaching of most Ca-ions.

When determining Ca_{ex} concentrations on the flame photometer, results were not satisfactory as it could only

be worked on a limited part of the range, probably due to interference of the high sodium concentration of the used solvent (0.5N sodium acetate). The results showed very high Ca_{ex} concentrations in the O-horizons; 5200ppm for profile 1, 5500ppm for profile 2, 1160ppm for profile 6 and 2700ppm for profile 7. Values for the A_1-horizons were of similar magnitude for profile 3 (5800ppm) and profile 2 (4600ppm), but much less for profile 1 (850ppm), profile 4 (550ppm) and profiles 5,6,7 (400, 400, 449ppm). There were still 100ppm Ca_{ex} in the 10-20cm samples of profile 1 and 710ppm at the same depth of profile 3, but otherwise concentrations were zero. It is not known whether these data represent the actual Ca_{ex}values of the samples, but at least the data for the A_1-horizons reveal the same mode of a rise from profile 1 to 3 and then decline to profile 4 and 5,6,7 which have about equal values.

5. SUMMARY OF THE SOIL INVESTIGATION

The seven investigated soil profiles can be arranged in a tentative chronosequence on the basis of their geomorphological position and state of the present profile development. This relative time sequence generally confirms the ordination assumed beforehand according to the actual vegetation cover of the sites with the exception of profile 4 which may be placed between 6 and 7. Unlike the others, this site does not support subalpine forest but merely scrub which was also burnt in the late 19th century thus rendering direct comparisons more complicated.

Profile 1 is a relatively young terrace soil of the Tasman set; a minimum age of 200-250 years seems to be indi-

cated by the present vegetation. A and B-horizons are developed to a depth of 25cm only, the underlying alluvium still contains the presumed original phosphate content of 470ppm, 250ppm of which can be designed as P_{inorg} (soluble in 1N H_2SO_4). Total nitrogen, P_{ex} and K_{ex} reserves are still low to medium. This site does not receive any nutrient influx from the adjacent higher terrace because a small flood channel, running parallel to the slope catches and diverts all runoff.

Profile 2, also on a terrace, is somewhat older but does not show signs of pozolization and may still be termed Tasman soil. Its profile is developed beyond 50cm and its nutrient status is generally higher compared with the former profile. This site may have an additional nutrient influx from runoff draining the adjacent hillside.

Profile 3 has the most fertile topsoil of all sites. It is situated on the site of an old slip that left a large depression in the slope. Its bottom is probably filled with loose talus allowing free subsurface drainage bringing additional nutrients from higher altitudes. This profile shows a discolouration by leaching below the A_1-horizon and can therefore be recognized as a high country podzolized yellow-brown earth like all the older profiles.

Profile 4 is the already mentioned controversial site on a fluvioglacial terrace with a recent fire history. Its original N and P reserves may have been depleted by the burn and part of it may have been washed out into the lower parts of the profile where it became fixed again to organic matter and clay particles. Exchangeable Ca and K, possibly derived from the plant ash, seem to have behaved in this manner.

Profiles 5,6, and 7 are of very similar appearance, they show distinct A_2-horizons, their nutrient status is clearly ranging below that of profiles 1,2, and 3, only the N, P_{ex}, and K_{ex} values surpass those of the youngest profile at site 1.

C H A P T E R V

COLLECTION OF CLIMATOLOGICAL DATA AND THEIR INTERPRETATION

1. INSTRUMENTATION

Air temperature was recorded on Casella thermohygrographs placed in a standard screen at a height of 1.5m above the ground. The record charts were usually changed at weekly intervals. In combination with the thermohygrographs, soil thermographs (Negretti and Zambra) with two sensors were installed at each of the climate stations. One of the sensors was placed 2cm above the ground to record the temperature near the soil surface, the other was placed horizontally into the soil at 15cm depth. Additionally, minimum-maximum thermometers (mercury in glass) were placed near the sensor at ground level and next to the thermohygrographs in the screen in order to check the accuracy of the thermographs. The thermometers, in turn, were collected about every three months and calibrated.

Initially, in September, 1982, five such combined climate stations were set up in the vicinity of the Pegleg Creek - Otira River confluence in places where growth measurements were to be carried out later on (figure 18). However, when it was recognized that the particular "mesoclimates" of the sites did not differ markedly, three of these stations were dismantled at the end of April, 1983, also because the maintenance of five stations was too time-consuming. Only station 1 and 2 were left working after April, 1983. Station 1 was the "reference" station, situated at 860m a.s.l. in open scrubland to record the actual air-temperature that

could be compared with the readings of the official meteorological stations at Arthur's Pass village and Otira. Station 2 was set up under the dense canopy of a grove of original subalpine low forest, spared by the late 19th century fires.

Station 1 and 5 were additionally equipped with standard raingauges (12.7cm diameter, collecting type). The raingauge at station 5 was later removed because it was unsuitably placed. The rain catches were measured weekly and at the 1st of each month to get exact monthly rainfall data.

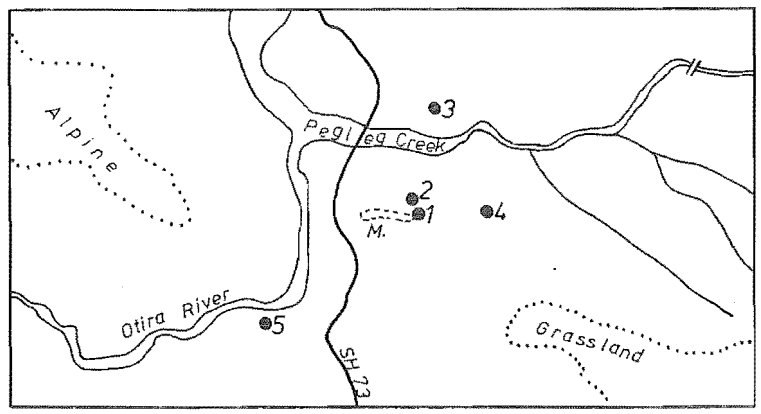

Figure 18. Location of the five climate stations.

The temperature traces on the charts were transferred to daily maxima, minima and mean tables. The mean daily temperature was calculated as $\frac{\max + \min}{2}$.

Copies of the daily readings of the climate stations at Arthur's Pass and Otira were obtained from the New Zealand Meteorological Service for comparison with the Pegleg Flat data in order to establish lapse-rate values. Long term records of monthly means, also provided by the Meteorological Service, were then used to calculate the approximate mean monthly and annual temperature and precipitation data for the study site at Pegleg Flat.

2. SCREEN TEMPERATURE

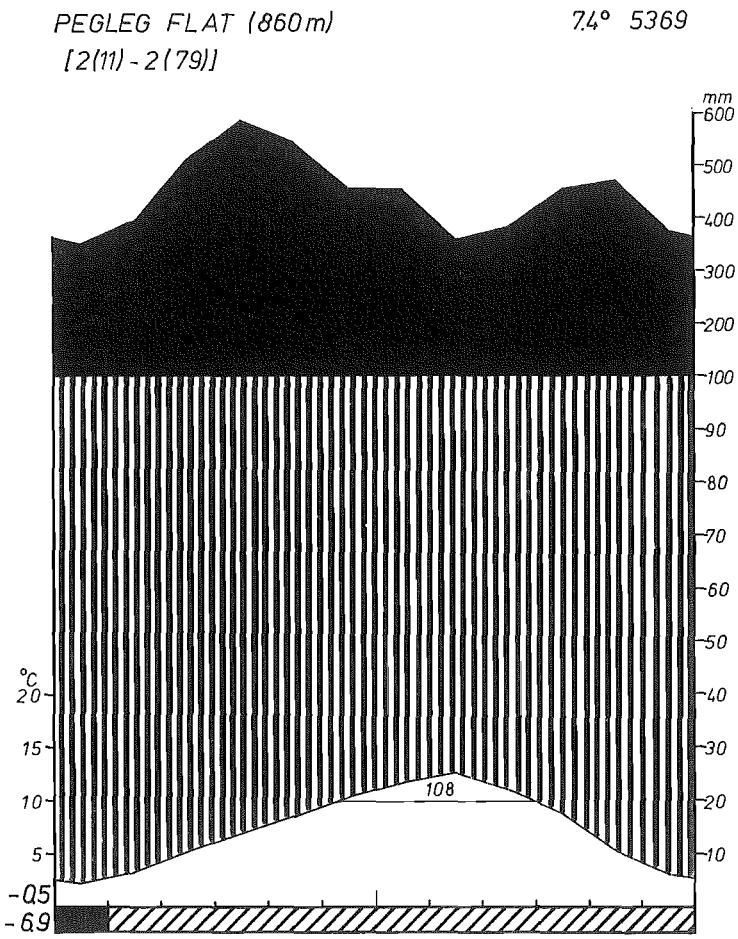

Figure 19. Climate diagram for the investigation area.

Legend:

Top left: station, altitude, years of observation (temperature - precipitation), Otira records in brackets.

Top right: mean annual temperature, mean annual precipitation.

Solid black: curve of mean monthly precipitation above 100mm, scale reduced to 1/10th.

Hatched area: curve of mean monthly precipitation, scale in proportion 20mm = 10^{o}C.

Bottom: curve of mean monthly temperature, the number of days with a mean temperature above 10^{o}C is indicated.

Bar at bottom: solid black - months with mean minima below 0^{o}C. hatched - months with absolute minima below 0^{o}C.

-0.5 - mean minimum of the coldest month, -6.9 - lowest recorded temperature.

Though only the records of two years'on-site temperature measurements were available, calculated data for an additional nine years were obtained after appropriate conversion of the readings of the Arthur's Pass and Otira stations. An annual mean screen temperature of 7.4°C was thus established for the investigation area. The curve of the mean daily temperatures is skewed, February being the warmest (12.5°C) and July the coldest month (2.4°C). There is a very constant rise of mean daily temperature of 1.7°C per month from August to December, smaller rises are evident from July to August and from December to February. Mean air temperatures are falling from February to July, the by far greatest monthly decline is from April to May (3.5°C). During the period of direct measurement (September, 1982 - May, 1984) the highest recorded temperature was 24.4°C (January, 1984) and the lowest -6.9°C (July, 1983).

Table 3. Calculated mean temperatures and precipitation.

J	F	M	A	M	J	J	A	S	O	N	D	Year
11.6	12.5	11.0	8.7	5.2	3.0	2.4	3.4	5.1	6.8	8.5	10.3	7.4°C
455	361	384	458	472	377	354	399	517	590	546	456	5369mm

When dealing with climate - vegetation relationships annual mean temperature is usually given for the July-June period because this is centered around the Southern Hemisphere summer and therefore gives better information concerning the quality of the particular growing season. Figure 20 shows two major deviations from the 11-year mean, the unusually warm 1974/75 season and the very cool 1982/83 season which was experienced during the field study.

Frosts are not unusual throughout most of the year

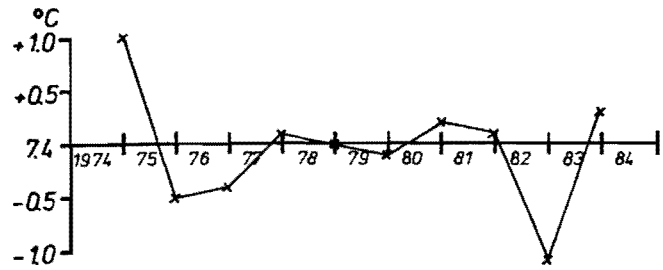

Figure 20. Variation of the annual mean (July-June) at the investigation area at Pegleg Flat.

though seldom severe. During 1983, minimum temperatures were below zero on 46 days (see table 4). The only month with a

Table 4. Temperature records below 0°C during 1983.

daily minimum of:	0-1,	1-2,	2-3,	3-4,	4-5,	>5°C below zero
number of observ:	20	16	2	5	2	1 days

mean monthly minimum below zero is July for which -0.5°C was calculated. Mean minima for June and August were found to be just above 0°C but longer records could possibly reveal below zero minima for both months. Occasional frosts are presumed to occur throughout the whole year. Though there were no recorded frosts at Pegleg Flat from December, 1982, to February, 1983, and from November, 1983 to March, 1984, the records of the Arthur's Pass station (available from 1978 onwards) point to light unseasonal frosts for each summer month and longer records will probably confirm this. The Arthur's Pass recording site is situated 5.2km south of Pegleg Flat at a lower altitude (738m) but on the "continental side of the Main Divide (figure 21). It has three winter months with mean minima below 0°C (June, -1.6; July, -2.0; August, -1.4°C). The lowest temperature on record is -8.8°C (May, 1978).

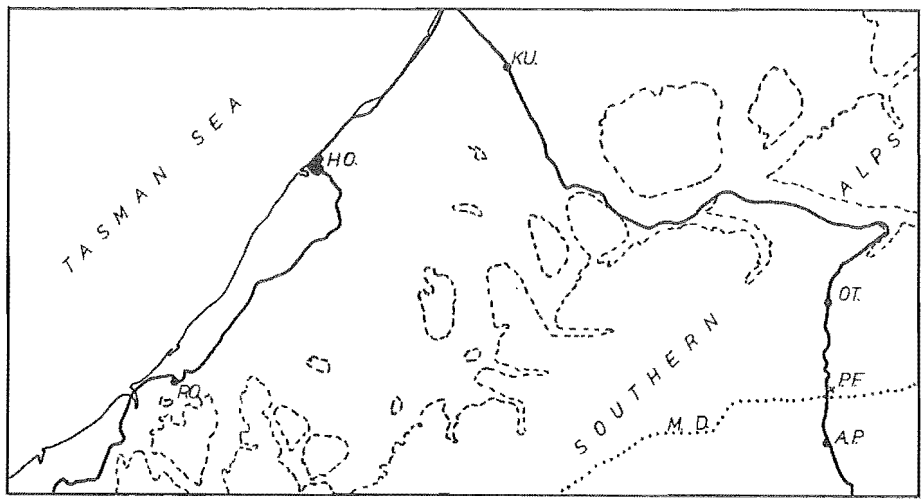

Figure 21. Map of north Westland and the Alps showing the location of the three mentioned climate recording stations with regard to distance from the coast, foot of the Alps, and Main Divide.

A lapse rate of 0.69°C/100m of the annual mean temperature can be calculated using the data of the Arthur's Pass and Otira records. But the two stations are situated at different sides of the Main Divide with different prevailing weather systems. Furthermore, the Arthur's Pass recording station is presumed to be situated in an unfavourable location with a great deal of obstruction from the surrounding steep mountains and possibly with ponding of cold air, especially in winter. A better estimate for the lapse rate may be obtained by comparison of the Otira and Pegleg Flat readings which will give a value of 0.51°C/100m. Garnier (1950) gives lapse rates for differnt parts of New Zealand for altitudes below and above 610m (2000ft) where he presumes a noticeable change in lapse rates. For the upland South Island these values are 0.27°C/100m for the lower altitude and 0.77°C/100m above 610m. The altitudinal difference between Otira (383m) and Pegleg Flat (860m) crosses this boundary, slightly more than half the distance being above it.

Thus an average lapse rate of 0.54°C/100m is obtained as a result of an integration of both sets of data, a value which compares well with my own findings. The empirical 3°F/1000ft equals 0.55°C/100m which is in accordance with the calculated lapse rate. During the time of direct recording at Pegleg Flat lapse rates were highest in January (0.73 and 0.67°C/100m) and lowest in June-July (0.38°C/100m). Lapse rates for the mean daily maximum temperature are higher (0.71°C/100m) than for the mean minimum temperature (0.29°C/100m). The highest lapse rates were calculated for the January mean daily maximum temperatures (0.90 and 0.92°C/100m) which is still slightly below the dry adiabatic lapse rate of 0.99°C/100m (e.g. McCracken, 1980).

3. MICROCLIMATE

Climate station 2 which was installed in a grove of subalpine low forest gave an annual mean temperature of 6.4°C for 1983 compared with 6.95°C for station 1. The forest cover also dampens down the mean daily range of temperature (4.4°C as compared with 6.5°C at station 1). Mean daily maximum temperatures of station 2 are considerably below those of station 1 (8.6°C versus 10.1°C) but mean daily minima are higher except for July and August*. Higher than average mean daily minimum temperatures were responsible for 0.2-0.3°C higher mean daily temperatures at station 2 during March to May, 1983.

The three remaining stations were only tended from September, 1982, to April, 1983. The mean daily temperatures

* Refer to appendix 3 for actual monthly mean temperature records.

for this eight months period are given in table 5. In the last column the mean daily temperature of the reference station 1 has been adjusted according to the actual altitude of the particular recording site using a lapse rate of 0.5°C/ 100m.

Table 5. Comparison of the microclimate at stations 1-5.

Station	altitude	mean temp.*	calculated**
1	860m	7.89°C	7.89°C
2	850m	7.86°C	7.94°C
3	910m	7.64°C	7.64°C
4	845m	8.05°C	7.97°C
5	835m	7.71°C	8.01°C

If only the eight warmer months of the year, which make up the growing season, are considered, the mean daily temperatures of all five stations are very similar because lower maxima are about equalized by higher minima. Stations 2-5 were all set up under forest cover which dampens the diurnal temperature range. Station 2 which revealed a 0.55°C lower annual mean temperature than station 1, now shows an almost identical mean temperature because the lowering effect of the colder winter months is excluded from the data. The effect of the forest cover only accounts for a decrease of 0.08°C. Station 3 can be more readily compared with station 1 because it was situated under a fairly open canopy of *Hoheria glabrata* forest. The lower mean temperature is

*average of mean daily temperature from September, 1982, to April, 1983.
**refer to explanation in the text above.

accounted for by the difference in altitude. Surprisingly, station 4 is slightly warmer than would be expected after the lapse rate calculation. It has lower mean maximum temperatures than both stations 1 and 2 but unusually high mean minima which may be explained by its sheltered position under dense *Dracophyllum traversii* canopy on a south facing slope. But as this site receives only little direct sunlight during the winter months the true annual mean temperature will tend to be much lower. Station 5 is 0.3°C colder than calculated, it shows the lowest mean maxima, and mean minima are also not markedly higher than at station 1. Obstruction of the solar path during the late afternoon in spring and autumn, and probably the situation on the river flat which allows ponding of cold air and a general cooling effect of the river could explain the lower temperatures.

4. SOIL TEMPERATURES

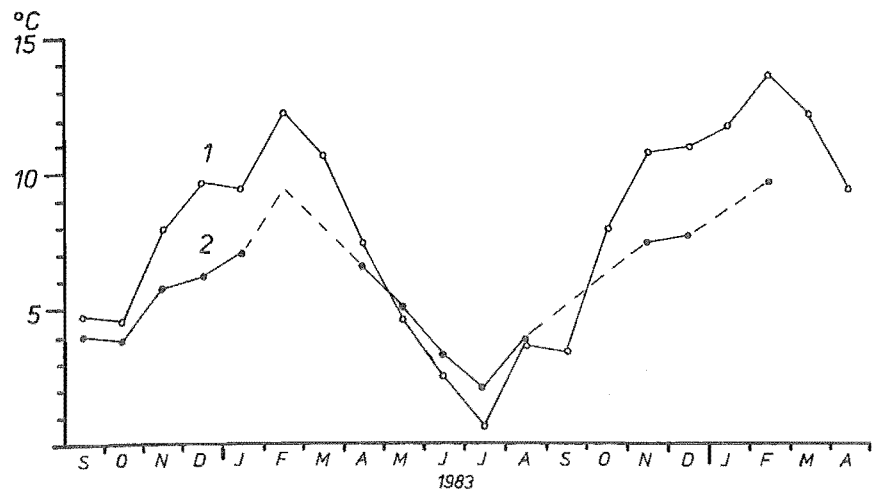

Figure 22. Monthly means of soil temperature at 15cm depth.

Mean daily soil temperatures at 15cm depth were found to be above mean air temperatures during the summer but below

these in winter. At station 2, however, the reverse applies. In the soil the daily temperature regime is dampened down and diurnal variation ranges from 0.6°C (July, station 1) to 2.1-2.3°C during the summer months. Under forest (station 2) the mean daily variation was far less, never exceeding 0.6°C. The annual mean for 1983 was 7.0°C at station 1, i.e., almost equal to the screen temperature (6.95°C).

5. PRECIPITATION

The relatively short time of rainfall monitoring at Pegleg Flat on its own would not give a satisfactory figure for mean annual precipitation. However, as it was supposed that precipitation at the investigation area would be related to the Otira rainfall, 37 weekly to fortnightly catches were compared between both stations, allowing the calculation of 105.8±5.7%* of the Otira catch for Pegleg Flat. The figure for 1983, which was directly compared, was 103.2% which is well within the limits of variation. On the basis of the Otira mean of 5075mm the mean annual precipitation for Pegleg Flat was then calculated to be 5369mm. The same procedure was employed for the monthly means. Monthly figures may be slightly higher in summer and lower in winter, but no exact data are as yet available. The rainfall graph (table 5;figure 19) shows one distinct spring maximum with October being the wettest month (590mm) closely followed by November (546mm) and September (517mm). December and January are still slightly above average (456, 455mm) and there is another maximum during April-May (458, 472mm). Consequently,

* mean and standard error; P 0.05

there are two drier than average periods, firstly, the three winter months with less than 400mm each of which July proves to be the driest (354mm); the other minimum occurs in February -March (361, 384mm). As the Otira figures indicate, monthly falls vary considerably, highest monthly totals have exceeded 900mm in any month and 1100mm from September to February and in May. The highest figure being 1505mm for October. Minimum figures are still at least 100mm from September to November, but less than 10mm in June and July. Months with minimum precipitation are much less common than months with exceptionally high rainfall. Annual totals for Otira range from 3568mm (1930) to 6813mm (1928). 1983 proved to have the second highest total on record (6621mm) while 6831mm were recorded at Pegleg Flat during the same year.

At Pegleg Flat, snow fell on at least seven occasions during the winter of 1983, most of it in June and September, the rest during July and August, but it contributed only about 1% towards the total annual precipitation. Usually, snow only remains on the ground for two or three days to one week at a time and is therefore not supposed to play any important part in the ecology of the vegetation except for the occasional heavy falls of wet snow that cause snow-break in the forest canopy.

6. WIND SPEED AND WIND DIRECTION

Wind speed was not measured at Pegleg Flat but records available from the Arthur's Pass station are thought to be comparable. Because of the general S-N extension of the Bealey - Otira valleys, only two prevailing wind directions

can be distinguished. Winds from the northerly quarter are by far the most prominent. During the period of observation from September, 1982, to April, 1984, i.e., 608 days, northerlies were blowing on 391 days (64.3%), southerlies on 119 days (19.6%), and only 98 days were calm (16.1%). Out of the 510 windy days 359 (70.4%) were in the range of wind force 1-3 and 151 (29.6%) had force 4-7. Days with wind force 8 and above were recorded on two occasions at the Otira station only. Local light winds affect the investigation area during otherwise still weather - flowing down the Pegleg Gorge at night and upslope during daytime (C.J.Burrows, pers.comm.).

7. SUMMARY OF THE CLIMATOLOGICAL STUDIES

Collection and interpolation of climatological data reveal a cool temperate and superhumid climate for the investigation area. The monthly mean air temperatures range from 12.5°C in February to 2.4°C in July resulting in a relatively flat annual temperature curve typical for oceanic climates. Frosts may occur throughout the year but are never extreme. Only 108 days of the year have a mean air temperature above 10°C (mid December to the end of March), whereas 222 days are above the 6°C limit often connected with the growing season (e.g. Ford, 1982). The calculated temperature curve shows this to be from end September until the first week of May which coincides perfectly with the field observations on plant phenology at Pegleg Flat.

C H A P T E R VI

MEASUREMENTS AND OBSERVATIONS OF PLANT MORPHOLOGY AND GROWTH

1. METHODS OF PLANT GROWTH MONITORING

(1) Measurements of seasonal increment growth

Dendrometers were made and fitted to the stems of *Hoheria, Olearia* and *Dracophyllum* in order to obtain continuous data of radial stem growth. The dendrometers were made after a model provided by D.Norton (Norton, 1983b) but aluminium was used instead of stainless steel and they were equipped with a millmetre scale. The dendrometers were fixed around the tree trunk by thin steel wire that was held in place by two or three staples. As a certain minimum diameter is necessary to ensure proper working the dendrometers were placed as low as possible at the base of the trunks to take advantage of the larger circumference. Height and circumference at the position of the dendrometer were noted and the present reading of the vernier scale was taken to the nearest 0.1mm. Further readings were made at fortnightly intervals throughout the growing period and about monthly during the cool season.

The stems of *Senecio bennettii* are too thin to hold a dendrometer and therefore *Senecio* could not be considered for this particular study.

(2) Coring of stems for determination of average annual growth and maximum age

In order to estimate the average annual radial increment and the approximate age of the species, a number of in-

crement cores were obtained using a Swedish increment borer. The trees were cored immediately above basal buttress-like features and only one core per tree was taken. The holes were sealed with vaseline jelly. Height above ground and circumference of the stem at the position of the core sample was measured as well as the total height of the sample tree. The cores were stored in commercial drinking straws. The cores were then cut longitudinally with a sharp carving knife blade for better interpretation. When using sandpaper to get a smooth surface, the large earlywood vessels of *Hoheria* and *Olearia* fill up with wood dust making them less conspicuous.

The number of growth rings was counted and the total length of the core determined, allowing the calculation of the actual age of the tree and average annual increment. In cases where the pith was missed or heartrot had occurred the number of missing rings was roughly calculated and added to the counted ones.

A few trees and shrubs uprooted by slips or windthrow were cut and a slice taken for additional information on radial growth and age. Some seedlings and saplings were cut to estimate their age and radial and height growth.

(3) Measurement of shoot growth and leaf area growth

Senecio bennettii is so abundant in the area that there were no problems in finding enough individuals to sample on a statistically sound basis. Tagging of shoots was carried out in August and September, 1982, and 1983; at each site, ten apparently healthy looking shrubs of average size were chosen within an area of approximately 10 x 10m for the purpose of growth monitoring. Five shoots per shrub were tagged with a

piece of blue nylon string (the number of knots ensured individual re-identification of the five tagged shoots), and the following set of data was obtained immediately: number of leaves grown in the previous summer and the summer before; lamina length of each individual leaf; shoot length of the previous season and, if possible, earlier seasons; number of sidebranches produced during the last three seasons. The shrubs were then checked at weekly to fortnightly intervals and the date of bud swelling and first leaf emergence ascertained. Thereafter, leaf length of the currently produced new leaves was measured at fortnightly intervals, as was increase in shoot length. The remaining older leaves were also counted each time to estimate the litter production per shoot.

At the end of the growing season, when no further leaf growth could be detected, the complete shoots were harvested and transported to the laboratory in airtight plastic bags. For determination of leaf area the leaves were detached from the shoot, the individual lamina length was noted, and the area of each leaf was determined with a LI-COR areameter. The complete leaf area produced during the just completed growing season was determined and the area of the still remaining older leaves was added to give the actual leaf area at the date of collection.

As only lamina length could be measured during the growing season it was necessary to establish a leaf length - leaf area relationship for conversion of the field data into the ecologically more relevant leaf area dimension. This was done by plotting the data-pairs of the harvested leaves on a graph which was subsequently used to convert the leaf length measurements into leaf area values. Usually, indi-

vidual graphs had to be plotted for each of the shrubs.

The leaves of each shoot were then separated into the two different age classes and oven-dried at 105°C. After cooling in a desiccator the dry weight was determined. The leaves were than ground in a mill and stored for further analysis.

Olearia ilicifolia is restricted to certain sites and is less abundant in the investigation area than *Senecio*. Furthermore, juvenile individuals are very rare and all the measurements taken continuously during the season had to be done on mature trees of 4-6m crown height. These fully grown trees had to be climbed to take the actual growth measurements of the canopy foliage, therefore, all individuals which could not be climbed fairly easily could not be considered for the study and only five trees at each site were dealt with. All measurements and data treatments were performed as with *Senecio*.

The climbing and tagging of trees proved nearly impossible for mature *Hoheria glabrata* individuals. The apex of leading shoots frequently dies back leaving the main stem with rotting heartwood and so fragile that it cannot be climbed in most cases. New growth only takes place at the branch tips that are usually beyond the reach of the investigator. Only a few mature individuals, growing close enough to other trees - usually *Olearia ilicifolia* - could be included in the study. Most of the research was therefore carried out using juvenile trees.

Different methods had to be applied when studying the growth of *Dracophyllum traversii*. The leaves grow for four to five seasons until they reach their final length and all

leaves are arranged in terminal whorls at the tip of the branchlets, the internodes being very much suppressed. Five shoots were tagged per tree and the number of leaves per shoot counted. Then five of the younger still growing leaves were marked with a waterproof felt-pen and their initial length measured with a piece of metal tape that had its end cut in a triangular shape so that it could be pushed under the leaf until it met the stem. To estimate annual production of new leaves, the fifth youngest leaf of each tuft had its tip marked with a marker-pen, the younger ones being situated too deep in the tuft to be conveniently marked. Some of the oldest leaves were also numbered to check litter production throughout the season. The trees were re-visited once a fortnight and the actual length of the marked leaves measured. The number of newly formed leaves and the number of shed leaves was also ascertained. The above described method of leaf measurement may give an individual error of one to two millimetre depending on the force used to insert the metal tape into the tuft but as 50-75 leaves were checked at each stand, the sample mean would be quite reliable. This was proven when almost identical growth rates were calculated for a number of successive fortnightly periods. The leaf length measurements were later converted to leaf area values.

(4) Shoot growth of previous seasons

Annual shoot growth of several past years can be easily recognized in *Hoheria glabrata*. The last leaf of the season, situated immediately below the resting bud, is usually very small and underdeveloped but nevertheless subtends an axillary bud. This particular bud never develops into a side-branch during the next season and can always be distinguished

from other buds by its very small or missing leaf scar. This feature remains visible for up to ten years before it gradually disappears as a result of radial growth. Approximate annual shoot length of still earlier years can be distinguished by the annually produced branch whorls just below the described mark because the two to four axillary buds next to the shoot apex are usually not suppressed and develop into sidebranches during the following season.

A crowding of leaf scars produced by shorter internodes towards the end of the growing season and remnants of budscales allow for determination of annual shoot growth in *Olearia ilicifolia*. These features are visible for two to three years only before being destroyed by stem expansion and production of secondary bark. The growth of a few more seasons may be recognized because the new shoot often grows with a slight angle and usually produces one to three sidebranches at its base.

In *Senecio bennettii*, only shoot length of the current and previous season can be determined by the presence of the small and often scale-like foliage leaves produced at the end of the growing season. Once these are shed, the stem soon produces secondary bark. Sidebranches are produced less frequently and can generally not be used to trace annual shoot growth.

No external indications of annual shoot growth are present in *Dracophyllum traversii*. A feature related to annual height growth, however, is the production of successive layers of the papery bark. This can be observed after removing the outer layer of ring scars left by the shed leaves. Growth of secondary bark can only begin after the

lower leaves - by then five to six years old - have been shed because the developing bark would separate them from the conducting tissue of the stem. As the number of leaves per tuft is assumed to remain fairly constant, shedding of leaves and subsequent bark production will be correlated with the number of new leaves produced at the tip, and hence, shoot growth. Measurements revealed that maxima and minima of shoot length estimated in this way are comparable between different shoots.

(5) Observation of phenology and seasonality

Throughout the field work notes on the phenology of the four species were made. Dates of bud break, flowering and fruiting were determined and the intensity of the flowering and fruit setting was estimated. The flowers of the particular sample trees were exactly counted or, when in great number, at least estimated. In the two composites numbers of florets per capitulum and capitula per corymb (panicle) were counted. The scarce but very conspicuous flower panicles of *Dracophyllum traversii* were counted throughout the investigation area using field glasses.

Insects presumed to act as pollinators or predators on the investigated trees and shrubs were collected and an attempt made to determine the genus or species.

(6) Use of sample plots for the floristic description of the different types of subalpine forest and scrub

Random sampling plots were laid out in appropriate stands of subalpine forest and scrub in which one or more of the considered species were sufficiently represented. Within these stands, 10 x 10m quadrats were marked with tape and the

orientation and aspect were determined using a compass; slope angle was measured with an abney level. General remarks like canopy height and vegetation layers were noted. The plots were then subdivided into four 5 x 5m subquadrats which were recorded separately. For each subquadrat, individual trees and shrubs were counted and their stem diameter and total height noted by employing a system of five size-classes ranging from <2cm to >20cm for diameter and from <20cm to >4m for height. The number of stems per individual was noted as single, double, triple or multiple. Presence of tree and shrub seedlings was observed and the ground cover was estimated on a percentage scale based on the Braun-Blanquet system.

(7) Monitoring of seedling survival under natural conditions

Wooden frames of 50 x 50cm dimension were fixed on the forest floor in October, 1982, in places where seedling germination was abundant. Occasional re-counts were made throughout the period of the field study and the number of the still surviving seedlings noted. Seasonal herb growth and litter cover within the quadrats was observed.

(8) Location of plots for seasonal growth studies

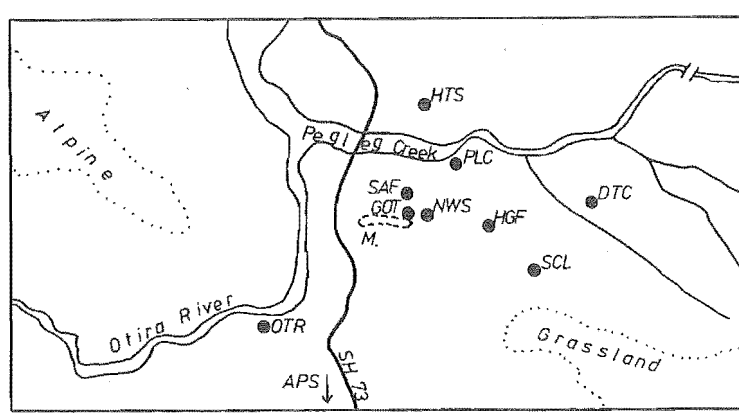

Figure 23. Location of the sites mentioned in the text.

The location of the sample plots where growth measurements were carried out are shown in figure 23. A three letter abbreviation was used to denominate the individual sites:

APS - Arthur's Pass Saddle
DTC - Dr. traversii clump
GOT - glacial outwash terrace
HGF - Hoheria glabrata forest
HTS - high terrace slope
NWS - NW-slope (Phipps Pk.)
OTR - Otira River
PLC - Pegleg Creek
SAF - subalpine forest
SCL - scrubline

2. TREE ARCHITECTURE

In the following section an attempt will be made to relate the characteristic growth habits of the four investigated species to the architectural models of tree growth that have been developed by Hallé, Oldeman and Tomlinson, (1978). Following the key provided by the authors, all four species show a differentiation into a trunk and branches, all vegetative axes are orthotropic and the terminal meristems have rhythmic growth. A division may be made according to terminal and lateral inflorescences which leads to the models described by Scarrone (1964, 1965, 1966) for *Dracophyllum traversii* and Rauh (1939) for all others.

(1) *Hoheria glabrata*

Hoheria glabrata fully fits the description of Rauh's model. According to Hallé, Oldeman and Tomlinson (1978) this model is most frequently encountered among seed plants and is very common among trees of high latitudes. The architecture is determined by a monopodial trunk with rhythmic (seasonal) growth. The branches are orthotropic and reveal the same growth characteristics as the trunk itself. Branches of all

orders are formed by proleptic growth, i.e., a discontinuous development of a lateral from a terminal meristem with an intervening period of rest. Thus branches are always formed from axillary (lateral) buds of the previous season's shoot, and the axillary buds formed in the current season need to overwinter before resuming growth. Usually only two, three or four axillary buds next to the apical (terminal) bud develop erect branches that show grotwh characteristics and extension growth rates comparable to the apical shoot. The axillary buds situated at the lower part of the shoot show a more and more suppressed growth, they may give rise to short lateral shoots that normally abort at the end of the growing season, or the buds may remain dormant altogether to abort some time later. The tree trunk and the main branches thus develop annual tiers of branches or higher order branches that clearly reveal the actual age and seasonal extension growth of the particular specimen. With increasing branching order the branches take over the habit of short shoots with minimal extension growth and a more or less plagiotropic orientation with the main purpose of supporting foliage leaves. The flowers are born laterally and have no significant influence on the tree architecture as a whole. Though most lateral meristems are exhausted in the process of flowering the axillary buds of the uppermost leaves are always spared and will produce the characteristic branch tier in the following season.

Though Bussell (1968a) states that there is preformation of leaves in *Hoheria glabrata*, the late season's growth may be by neoformation. Bussell gives a number of 6-10 leaves, recognizable in the apical resting bud, and found

Figure 24. Young specimen of *Hoheria glabrata* showing the typical growth habit; six tiers of branches are visible.

that no additional leaves are formed during the summer. At the Arthur's Pass trials, however, up to 17 leaves per apical shoot were frequently encountered, the uppermost usually unable to attain full size before being shed again. This rather suggests neoformation of the later leaves but it may be restricted to saplings and younger trees only.

The architecture described above is best revealed in saplings and young trees. With increasing age of the trees, and especially in the marginally suitable environments towards the alpine timberline, resting buds as well as complete shoots may die back more frequently, mostly by desiccation, and the growth habit is more and more determined by vegetative regeneration processes. After abortion of a terminal

bud, one or more of the uppermost lateral buds take over the growth habit of leading apical shoots. This results in a "bayonet-joint" morphology (Hallé et al, 1978) which is most frequently encountered in nature. The subordinate branch formed by an axillary bud would normally describe an arc to gain some distance from the superior apical shoot before taking over a more or less orthotropic growth habit. After the death of the apical meristem, however, the lateral branch is released from some kind of suppression and can take up the orthotropic habit straight away to occupy the space normally assigned to the apical shoot.

In most deciduous trees lateral buds will usually survive the more sensitive terminal buds when exposed to extreme enviromental conditions. Lateral buds are less developed and probably in a deeper state of dormancy, making them more resistant to desiccation and lower temperatures. The differences in low temperature tolerance are approximately in the order of $5^{o}C$ (Larcher, 1976, p.273).

When dieback occurs on a major scale, renewed growth can take place from dormant buds at the lower parts of trunk and branches. This results in the growth of stem suckers that repeat the juvenile growth habit. All leaves of suckers arise by neoformation throughout the growing season and shoot growth is indeterminate. It ceases late in the season when adverse climatic conditions set in. This was observed in late May to June, 1984, when suckers, arising from stumps after the cutting down of trees along State Highway 73 during December, 1983, retained their green foliage until the leaves died after freezing. The sucker shoots show an accelerated extension growth and annual rates of 30-50cm and possibly up

to 1 metre may be encountered. With new growth originating from suckers the old trunk may consist mainly of dead and decaying wood only.

Under natural conditions mechanical injury of *Hoheria glabrata* may be caused by windbreak, rockfalls, avalanches and flooding of rivers and *Hoheria* is very well adapted to survive these adverse conditions by its ready regenerative ability. The kinds of disturbance mentioned are always related to accelerated mineral inputs in the course of erosion and re-deposition of soil and rock debris, which suits *Hoheria's* higher nutrient requirements. Places of extreme disturbance like avalanche tracks and the related deposit areas are usually taken over by thickets of *Hoheria glabrata* which may survive here even with most of its bark stripped off by avalanches. This was observed in several places along the Milford Track where avalanches are a common feature.

Figure 25. Dense growth of *Hoheria glabrata* in a steep gully.

(2) *Olearia ilicifolia* and *Senecio bennettii*

Both *Olearia* and *Senecio* fit Rauh's model only when their early stages of growth or the growth habit of a single shoot apex are considered. The tree architecture of the adult individuals, however, cannot be categorized into any of the models described by Hallé et al (1978). Hallé's terminology is based mainly on studies of trees, whereas *Olearia* and *Senecio*, though of relatively large size, must be regarded as shrubs that show a less clearly defined differentiation of trunk and branches. *Olearia ilicifolia* often lacks a defined monopodial trunk. Branching usually occurs between ground level and three metre height resulting in a forked trunk, the main branches are casually forked again and again, ultimately forming the flat umbrella-like crown. This mode of branching is still more expressed in *Senecio*. This shrub, when growing in the open, always develops a spherical umbrella crown. Inside the subalpine forest lower branches of older specimens are soon lost because of lack of sunlight resulting in a better differentiation into trunk and branched canopy.

Unlike *Hoheria* which always maintains its orthotropic growth character - even the branches of blown over trees immediately resume growth in a vertical position - both *Senecio* and *Olearia* (mostly of hybrid character) often show a prostrate to procumbent growth habit of their main stems, especially when subjected to heavy shading inside the forest. The stems then develop a habit of "downhill layering" until finding a suitable canopy gap.

In both species shoot growth is orthotropic and monopodial, i.e., the apical meristem resumes growth after the

Figure 26. Young sapling of *Olearia ilicifolia* (Rolleston River catchment).

Figure 27. Shrub of *Senecio bennettii* showing the typical growth habit (scrubline at Arthur's Pass).

resting period. Branching is proleptic in *Olearia* with all shoots arising from the resting buds of the previous season's foliage leaves. This is generally true for *Senecio* as well, where the lateral branches are supported by the small scale-like leaves of the preceding season. But in some cases when two sidebranches are produced, and in any case for a possible third branch, the latter are formed by sylleptic growth from the axils of developing leaves of the current season. Lateral shoots in both composites are clearly distiguishable from the related apical shoot during the current season only, when the laterals have less foliage but show more extension growth. These differences vanish during the one or two subsequent seasons.

The foliage is only born at the tips of the branches which are more or less in one plane thus forming a one-layered canopy in the shape of a flat umbrella (*Olearia*) or "spherical umbrella" (Kugelschirmbaum of Troll, 1959) in the case of *Senecio* shrubs. This is understood to be a result of the heavy shading effect of the thick evergreen foliage. Shoots that fail to make sufficient progress of extension growth are quickly shaded and abort during the following season.

Flowering (see section 9) has no impact on the general architecture. Corymbs are born laterally in *Olearia* and may substitute an otherwise developed lateral shoot. The particular flowering modus of *Senecio* does not seem to be catered for in Hallé's terminology. When only the flowering shoot is considered the panicle is clearly terminal, leading to the subsequent abortion of the shoot, but if the particular shoot is regarded as a disposable short shoot flowering could be termed lateral.

There appears to be a peculiar periodicity with regard to the mean number of annually produced sidebranches per apical bud (figure 28). The same basic pattern is revealed at GOT and SCL though the former shows comparatively reduced figures from 1980/81 to 1982/83. It is therefore assumed that the activity of the lateral buds is in some way stimulatad by environmental conditions.

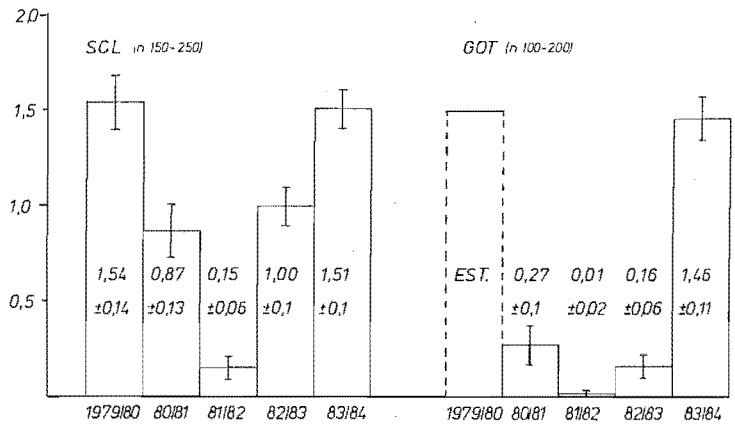

Figure 28. Seasonal variation in the number of lateral shoots formed per apical bud in *Senecio bennettii*.

Olearia ilicifolia has the ability to develop sucker shoots from dormant buds. Suckers occasionally grow from older branches of normally developed trees, they reveal a juvenile growth character with obviously indeterminate growth. Sucker shoots are much longer and have more leaves than normal canopy shoots. However, the foliage of these suckers does not receive enough incoming radiation for a sustained existence and will abort sooner or later. Older branches that were possibly derived from suckers have never been observed. Their successful growth will depend on opening up of the overhead canopy. Sucker shoots arising from older branches are

more common to trees at the forest margins where light levels are higher.

Sucker shoots can also be formed after mechanical injury. This was observed after the cleaning-up operations by the Ministry of Works along State Highway 73 in December, 1983. Some Olearias had large branches cut off and subsequently developed suckers close to the end of the stumps.

Senecio bennettii completely lacks this regenerative ability, most probably because no specialized resting buds are formed. Occasional growth of abortive miniature shoots is presumed to be a pathological feature (witches broom).

(3) *Dracophyllum traversii*

The growth habit of *Dracophyllum traversii* basically fits the model of Scarrone (described by Hallé et al, 1978). The architecture of this model is defined by an orthotropic rhythmically active meristem that develops an indeterminate main trunk with tiers of branches which are again orthotropic but sympodially branched as a result of terminal flowering. Though the growth of *Dracophyllum* is seasonal no special resting buds are formed and the branching pattern is neither annual nor is it much influenced by the dieback of terminal meristems after flowering. Flowers are only born on one to three per cent of the shoots each year and the shoots may not necessarily form sidebranches later on. In about half the cases the complete shoot down to its origin at the next lower order branch will abort. Dieback of terminal meristems and subsequent branching occurs frequently after the shoot apices have been predated or after mechanical injury. In most cases, however, branching is independent of the death of the apical meristem.

Figure 29. Sapling of *Dracophyllum traversii* showing tiers of branches.

Figure 30. Sapling of *Dracophyllum traversii* in dense subalpine scrub.

The basic architecture is most clearly revealed in saplings and poles which may nevertheless be 100-150 years old without becoming reproductively active. The straight growing trunk has developed several whorls of branches which repeat the same growth habit themselves. Between one and six branches may be present at each tier. Investigation of a number of saplings, most of which were between one and two metres high, gave an average distance of 28cm between successive tiers. This would indicate that branching occurs only once about every ten years. Sectioning of shoots revealed that sometimes a large number of axillary buds have formed initials of lateral shoots that aborted in an early stage of development. The lateral shoots have only short scale-like leaves at first and switch to normal foliage once they have grown out of the leaf tuft of the apical shoot. In older

Figure 31. Old individual of *Dracophyllum traversii* having lost its initial basic architecture after dieback of meristems.

trees this simple architecture is less obvious. The shoot apex of the main trunk has been lost in almost all cases, either by flowering, predation or mechanical injury (which is not surprising considering the age of 200-400 years), and has been substituted by several branches of approximately equal vigor making up the typical appearance of the tree, sometimes termed candelabra tree.

Dracophyllum traversii cannot form stem suckers. The axillary buds are lost when the leaf scars are separated from the stemwood after radial growth sets in. The buds are thus unable to outlive their axillant leaves.

Saplings growing in shady positions usually develop a procumbent stem which can run downhill for several metres but most of these individuals will be unable to survive in the long term unless considerable canopy gaps are formed in time. These procumbent stems do not develop adventitious roots.

Figure 32. Tuft of *Dracophyllum traversii* with three axillary branches after the shoot apex was destroyed by an unknown predator (note exit-whole in lower leaf).

3. ANNUAL WOOD INCREMENT

(1) Wood anatomy

A general description of the wood anatomy of the three arborescent species (*Hoheria, Olearia, Dracophyllum*) has already been given by Meylan and Butterfield (1978), another brief account can be found in Wardle (1963a). All three species have diffuse-porous wood. Annual growth rings are less easily distinguished than in ring-porous species. Though diffuse-porous, early wood vessels in *Olearia ilicifolia* are generally of greater diameter than later ones so that annual growth layers can be recognized. In *Dracophyllum traversii* and to a lesser extent in *Senecio bennettii*, the larger early wood vessels, though not individually distinguishable, often give the early wood a lighter colour. This gives a good contrast to the reddish brown late wood of *Dracophyllum*. Annual wood increment of *Hoheria glabrata* is made up of several successive layers of vessels, fibres and parenchyma (Wardle, 1963a). Usually the early wood vessels have a larger diameter than the subsequently formed ones but sometimes the growth ring boundary is hard to identify.

(2) Average ring width

Estimates for average ring width were attempted by Wardle (1960, 1963a) and the results of the present study were generally found to be in accordance with his data (table 6). The ring width of *Hoheria glabrata* mentioned in the 1960 paper of Wardle is a considerable underestimate but this was subsequently corrected (Wardle, 1963a). Annual wood increment in *Hoheria* and *Olearia* is of a very similar order (1.6, 1.7mm). All the *Hoheria* cores were taken from trees

at an altitude of 910m, i.e., 70-80m above the *Olearia* stands, so it may be supposed that at comparable sites *Hoheria* would tend to show the higher increment of the two. The ring width of *Senecio bennettii* is still in the same order (1.4mm) but all cored individuals were only about fifty years old and ring width will probably decline with age. The available data for *Dracophyllum traversii* coincide quite closely and clearly reveal the much smaller growth rate of this species. The graph of the stem diameter - age relationship (figure 33), though only based on scanty data, reveals a decrease in ring width with increasing age of the species tested.

Table 6. Mean width of annual growth rings

	(Wardle, 1960)	(Wardle, 1963a)	this study
Hoheria	0.7mm	3.0 (1-5)mm	1.6 (1.3-2.2)mm
Olearia	1.8mm	2.3 (1.3-3.3)mm	1.7 (1.0-2.4)mm
Senecio	n.d.	n.d.	1.4 (1.1-1.9)mm
Dracophyllum	0.5mm	0.55 (0.3-0.8)mm	0.5 (0.3-0.9)mm

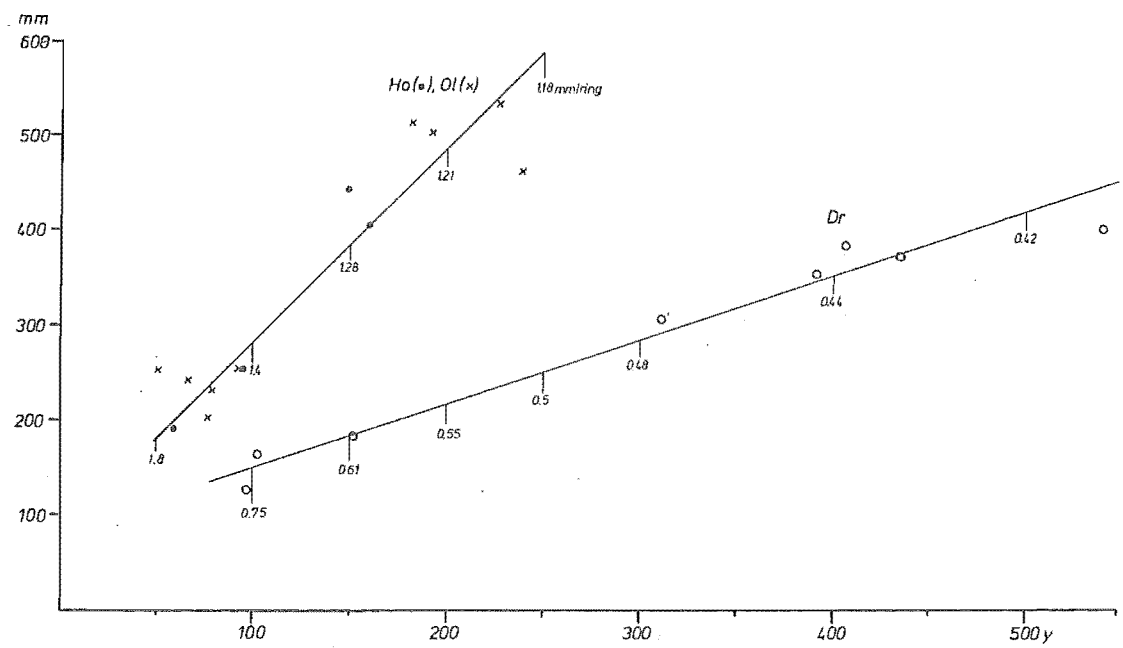

Figure 33. Age - diameter relationship in *Hoheria*, *Olearia*, and *Dracophyllum*; average ring width with age is indicated.

(3) Maximum ages of the subject species

Increment cores were taken preferably from mature trees in order to establish maximum ages for the species. These were found to be about 150 years for *Hoheria* and possibly up to 240 years for *Olearia*. Wardle (1963a) estimated 150 years and 200 years respectively. The maximum age of about 540 years for *Dracophyllum traversii* found in this study exceeds Wardle's maximum by 140 years. 476 rings were actually counted in this instance; the remainder is an estimate based on the presumed length of the missing part of the core and an addition of ten years for the growth to the coring height of 40cm. In four other cases, ages of about or slightly over 400 years were established.

(4) Seasonal cycle of wood increment

The seasonal cycle of wood increment could only be investigated in *Olearia ilicifolia;* the other species showed only very poor response to the type of dendrometers employed, which are probably not sensitive enough to record the slow diameter growth of *Dracophyllum traversii* and too large to be fitted properly around the comparatively thin *Hoheria* stems. In 1982/83, therefore, only the data for the *Olearia* stand at PLC (five trees) were of any value and the average circumference increase was calculated to be 3.0mm (figure 34). This gives a diameter increase of 0.95mm or 0.48mm ring width (based on an average circumference of 750mm). The growth lasted from mid November to possibly mid June. This rate is rather small compared with the average annual increment of 1.6-1.7mm but the growing season of 1982/83 was a particularly cold and wet one. The small number of sample trees may be another source of error. In the 1983/84 season increment

growth measurements were concentrated on *Olearia ilicifolia* with two dendrometers fitted to each sample tree and a more sensitive wire was used. Increment growth commenced in late October and lasted until the end of May or early June. The accelerated cambial growth in the trees at PLC in July and August will be discussed later as this is considered to be unseasonal growth. The trees at the PLC stand showed an average increase in circumference of about 5.9mm, i.e., a 0.95mm annual ring, if the increment in winter is excluded from the data. At OTR an average increase of 5.6mm was measured which is adequate to a 0.89mm ring. Maximum rates for single trees were 6.9mm (PLC) and 6.1mm (OTR). Though almost double the 1982/83 rate, these values are still short of the expected average annual growth. Part of the increment growth may probably escape the measuring device because of slack of the wire or jamming of the mobile scale but, on the other hand, both stands show the same general trend and the annual rates almost coincide. So it could be possible that the lower than average December and January temperatures may account for the low increment growth.

The trees at stand OTR have a slower start in November but reveal a remarkable acceleration of increment growth in January. Rates for the remaining months are comparable with those at PLC. The sudden upsurge in growth rates from end to mid January was clearly picked up by all of the seven satisfactorily working dendrometers at OTR but only by four out of seven at PLC.

The sample trees at PLC show accelerated cambial growth during July and, to a lesser extent, August. This increment was clearly registered on five of the employed dendrometers

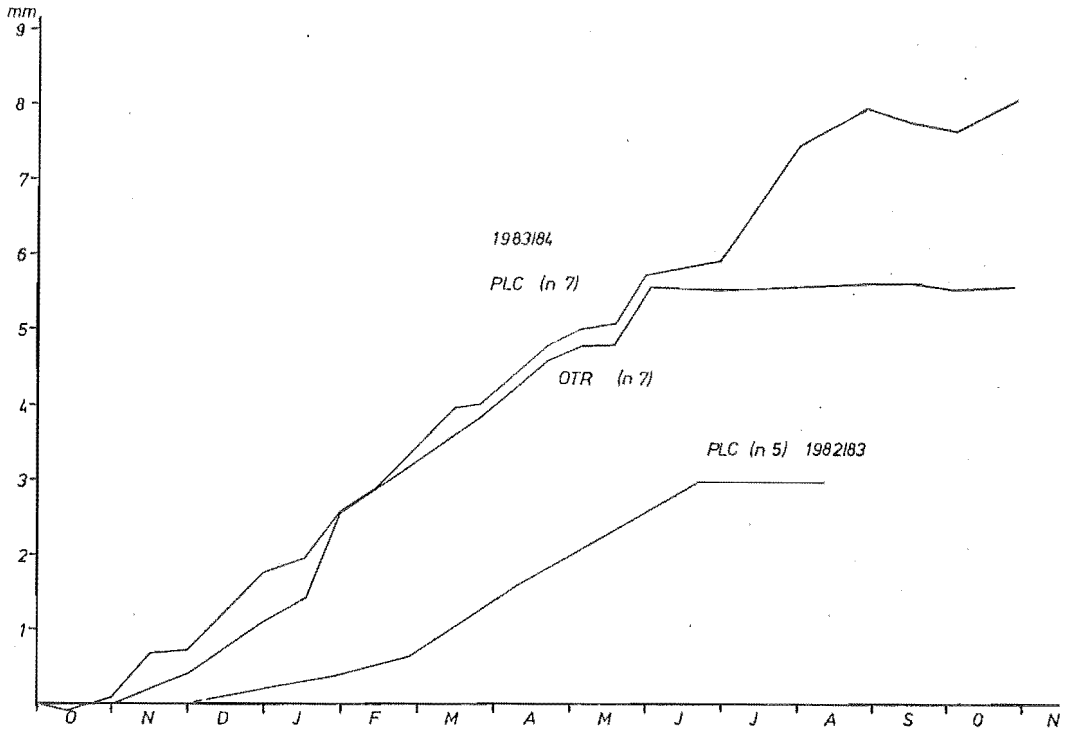

Figure 34. Seasonal circumference growth of *O. ilicifolia*.

with three of them giving readings of 2.0-2.2mm. The generally much older trees at OTR, however, did not respond.

Climatic records reveal the winter of 1984 as one of the warmest on record and the readings at Pegleg Flat, though incomplete, indicate mean temperatures around 5°C for June to August. This may have been sufficient to prevent the cambial activity from entering into the resting phase. As there was no carbohydrate expenditure for new shoot or leaf growth during this time most of the photosynthates were spent on further cambial growth. Sectioning of shoots of known ages showed that the continuing radial growth was an addition to the 1983/84 growth ring; growth of the 1984/85 ring started only in October after a short period of rest in September.

4. DESCRIPTION OF THE TYPES OF BARK

Hoheria glabrata has a grey bark which is retained during stem expansion. *Olearia*, *Senecio* and *Dracophyllum*

produce annual layers of a thin whitish (*Olearia*), yellowish (*Senecio*) or brown (*Dracophyllum*) papery bark. The old bark layers peel off and are shed in long strips in *Olearia* and in large flakes or pieces in the two other species. The steady peeling of the bark makes it an unsuitable habitat for epiphytes of all kinds. The green bark of the current season contains chloroplasts and is photosynthetically active in *Hoheria*, *Olearia* and *Senecio*; living bark of *Dracophyllum traversii* contains a red pigment.

5. ANNUAL SHOOT GROWTH

(1) *Hoheria glabrata*

Continuous shoot extension measurements were made for three stands of *Hoheria glabrata* during the 1982/83 season. In 1983/84 two of the stands (HGF and OTR) were substituted in favour of more accessible trees at the APS and PLC sites.

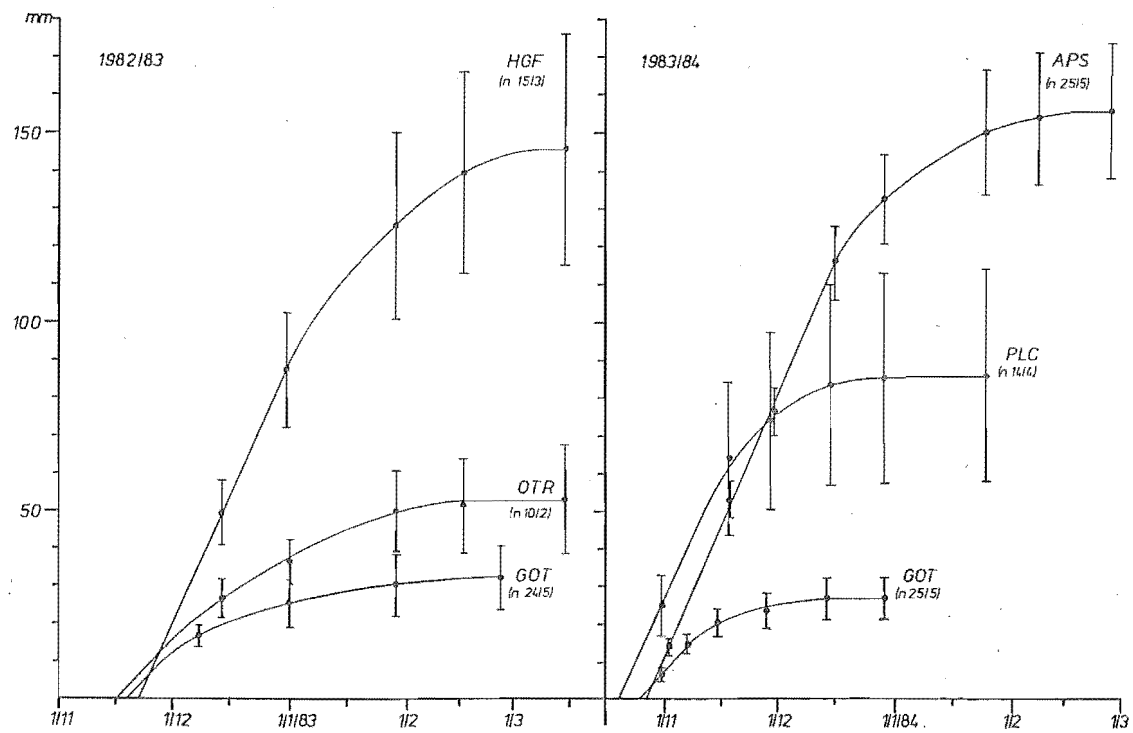

Figure 35. Seasonal shoot elongation in *Hoheria glabrata*.

In 1982 terminal buds opened and shoot growth began during the third week of November, starting slightly earlier at lower altitudes, i.e., approximately on November 16th at OTR (835m), November 19th at GOT (860m), and November 22nd at HGF (910m). Initial shoot growth was fast (2.25mm/d at HGF and 1.05-1.1mm/d at the other sites) but gradually declined soon after. Shoot growth ceased about February 20th at the OTR and GOT stands and about March 3rd at HGF. The total period of shoot growth was 104d at GOT, 107d at OTR, and 117d at HGF. In 1983 shoot growth started on October 19th at PLC (835m, saplings), October 25th at GOT (860m), and October 27th at APS (915m). Initial growth rates were 2.3mm/d at APS, 2.15mm/d at PLC, and 1.1mm/d at GOT. Shoot growth ceased earlier than in the previous season, on December 15th at GOT, December 25th at PLC, and about February 15th at APS. Total shoot length was considerably less than in 1982/83 in all cases and the growing season was shorter in spite of more favourable climatic conditions throughout most of the summer.

Hoheria glabrata seems to be particularly sensitive to spring temperatures. Growth trials by Bussell (1968a,b) showed that dates of bud break in 1963 and 1964 were farthest apart in *Hoheria* (about 20 days) as compared to the three other tested deciduous species. P.Wardle (1960) states that in the cold and wet summer of 1957/58 the leaves of *Hoheria glabrata* in the Toaroha River catchment (Westland) only expanded in December.

Shoot length of the last five seasons was measured at five different stands in the study area, and a similar pattern of annual growth was encountered in four of the five stands.

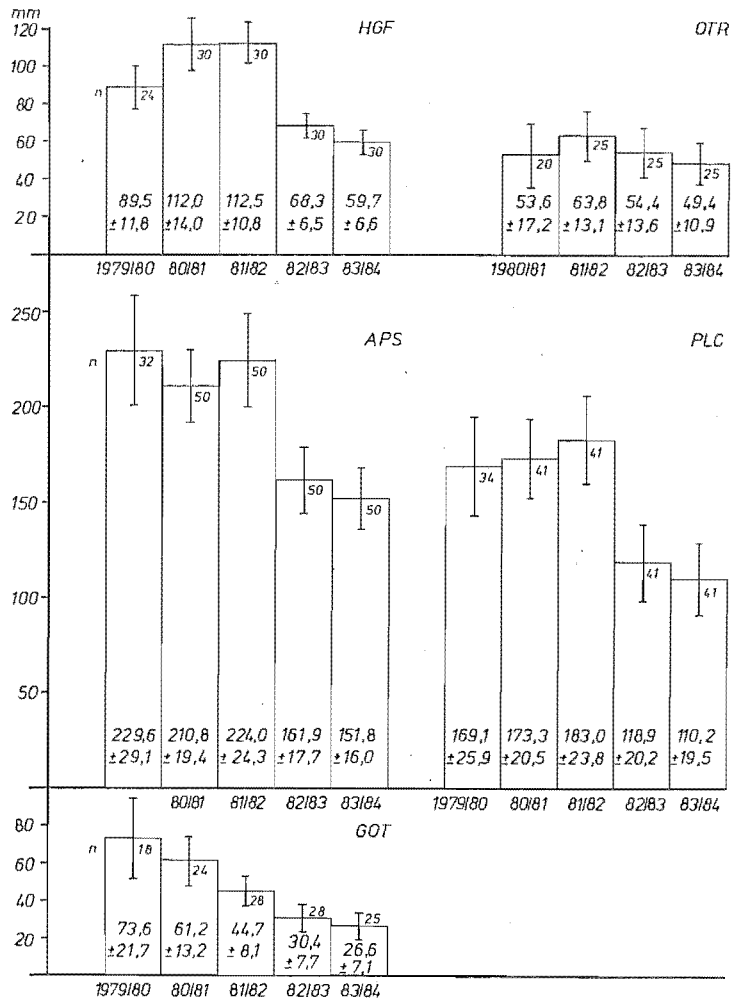

Figure 36. Average annual shoot growth in five stands of *Hoheria glabrata*.

In all five stands the 1983/84 season was represented by an overall low of shoot length, the 1982/83 season showed only slightly more growth (in the order of 7-14%). There was a considerable difference (usually 50% higher than the 1982/83 figures) to the 1981/82 season which produced the largest shoots during the investigated five year period. Shoots of the 1980/81 season were slightly shorter again in four of the sample stands and shoot length in 1979/80 seemed to be further reduced in two of the stands but was still considerably larger than in the 1982/83 and 1983/84 summers.

The growth of the trees at GOT does not fit the gene-

ral pattern as it shows a steady decline throughout the five year period. Environmental stress is clearly responsible. All Hoherias are rather young trees (20-30 years old) growing in the *Senecio bennettii* scrubland on the exposed terrace surface. Nutrient status of the soil is relatively poor as compared with other *Hoheria* stands and the porous texture does not support a high ground water level. During hot days, especially in February, the foliage, having no special xeromorphic structures, was seen wilting during the day. This drought stress has become more severe during recent years as the *Hoheria* saplings are beginning to emerge above the dense *Senecio* shrub layer and become steadily more prone to desiccation by increasing exposure. In several cases tips of branches were dead by March-April. A few trees in better condition can be found growing in the hollows - presumed to have been created by dead ice - were they are more protected from desiccation.

Average annual shoot length for *Hoheria glabrata* was calculated to be 150mm for juveniles and 75mm for adult trees. Bussel's trials were carried out in Dunedin gardens but his data for adult trees nevertheless compare satisfactorily. So do Wardle's results (see table 7).

(2) *Olearia ilicifolia*

Continuous shoot growth measurements were carried out at OTR and PLC using five sample trees in each location. The current growth from apical and lateral buds was measured individually. Though the lateral buds open a few days later and produce fewer leaves, they show higher rates of shoot extension growth (figure 37). Shoot growth of *Olearia* started during the first week of December in 1982 (data of OTR

point to the 5th or 6th of December, data of PLC indicate a period from the 28th of November to the 7th of December). Initial growth rates were 0.52mm/d (apical buds) and 0.71mm/d (lateral buds) at the OTR stand and 0.53mm/d and 0.5mm/d respectively, at PLC. Growth ceased after mid February. In the 1983/84 season shoot growth commenced at the 13th to 15th of November at OTR and at the 14th to 21st of November at PLC. Initial daily growth rates were smaller than those of the previous season, only 0.3mm/d (apical buds) and 0.35mm/d (lateral buds) at OTR, and 0.3mm/d and 0.49mm/d respectively, at PLC were attained.

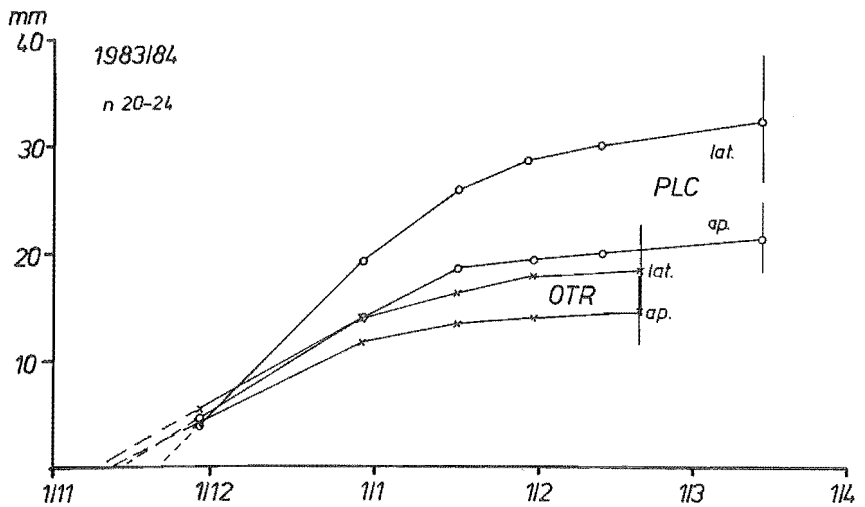

Figure 37. Seasonal shoot growth of *Olearia ilicifolia*.

Growth was terminated at about February 20th at OTR and March 10th at PLC. Total seasonal shoot growth lasted longer in 1983/84 (100-120 days) than in 1982/83 (70-85 days).

Average annual shoot growth for the last five years is given in figure 38. The data become less reliable with increasing age as it could not always be ascertained whether or not a certain branch had originated from an apical or lateral bud, thus figures for the 1979/80 and 1980/81 seasons

may be too high. For the two most recent seasons both apical and lateral shoots were investigated. In all cases the 1983/84 growth is well below the 1982/83 shoot length. Shoot length for the three seasons from 1980/81 to 1982/83 shows only insignificant variation and does not reveal any recognizable trend. Shoot length was highest in 1979/80 and even if minor reductions are taken into account (for reasons mentioned above) it should still represent the highest value for the five year period.

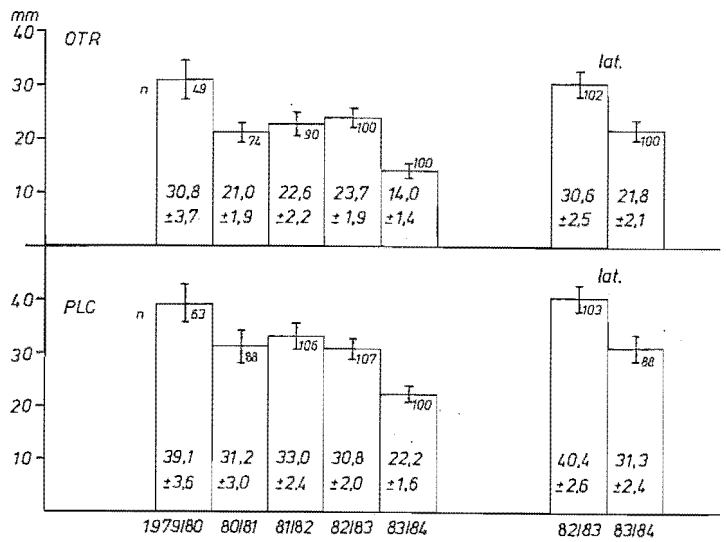

Figure 38. Average annual shoot growth during five years.

Shoot length of young saplings of 60-200cm height growing in the Rolleston River catchment at 800-850m altitude was also determined. The measurements gave an average length of 122mm for 1983/84 and 127mm for 1982/83. Very young saplings, less than ten years old, were measured on a recent terrace of the Otira River at Pegleg Flat and showed a shoot length between 88mm and 120mm (figure 39). In both stands of *Olearia ilicifolia* saplings the shoot length of the 1983/84 season is slightly but insignificantly reduced when compared

with the previous season. The difference of the means between the 1981/82 and 1982/83 seasons is significant at the 5% level.

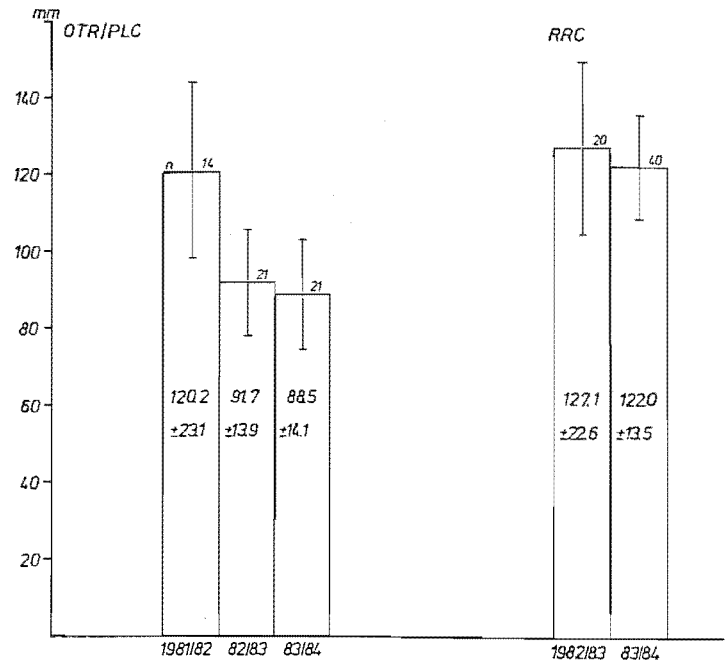

Figure 39. Average annual shoot growth of *Olearia* saplings.

Estimates of average annual shoot length for *Olearia ilicifolia* of 150mm (100-200mm) given by Wardle (1960, 1963a) most probably apply to very young specimens only. Mean annual shoot growth for mature trees at Pegleg Flat was a mere 27mm.

(3) *Senecio bennettii*

Records of continuous shoot extension growth of *Senecio bennettii* at GOT and SCL were made for the 1983/84 season only. Surprisingly, growth started earlier at SCL (ca. 1000m) than at GOT (860m). Though the apical buds open earlier than the lateral ones, extension growth of the lateral shoots is much faster and becomes easily discernible when the apical shoot

is still too short to be measured. Shoot growth started during the first December week with growth rates of 0.19mm/d (apical buds) and 0.38mm/d (lateral buds) at GOT, and 0.2mm/d and 0.35mm/d respectively, at SCL. These growth rates were kept up until the end of January when they declined apparently simultaneously to only 0.05 and 0.09mm/d (GOT) and 0.07 and 0.14mm/d (SCL). Extension growth ceased at the end of March lasting less than four months altogether.

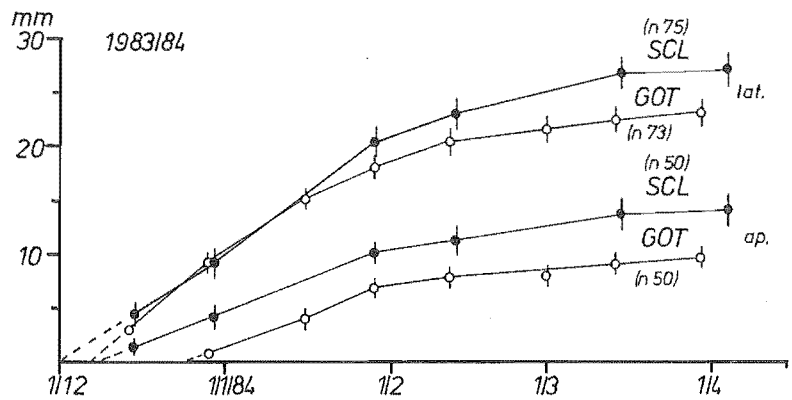

Figure 40. Seasonal shoot growth of *Senecio bennettii*.

Annual shoot length data were available from 1981/82 to 1983/84. There is a significant decline of shoot length to 1982/83 in both the SCL and HTS stands (difference of the means significant at the 2% and 1% level, respectively). A sharper decline took place from 1982/83 to the 1983/84 season, it is significant at the 0.1% level at stands SCL and GOT, but insignificant at HTS. The saplings at SAF reveal only this latter decline of shoot growth (significant at the 10% level); shoot length from 1980/81 to 1982/83 was almost identical.

The shrubs at GOT reveal the slowest growth probably owing to environmental stress by exposure, temporary drought

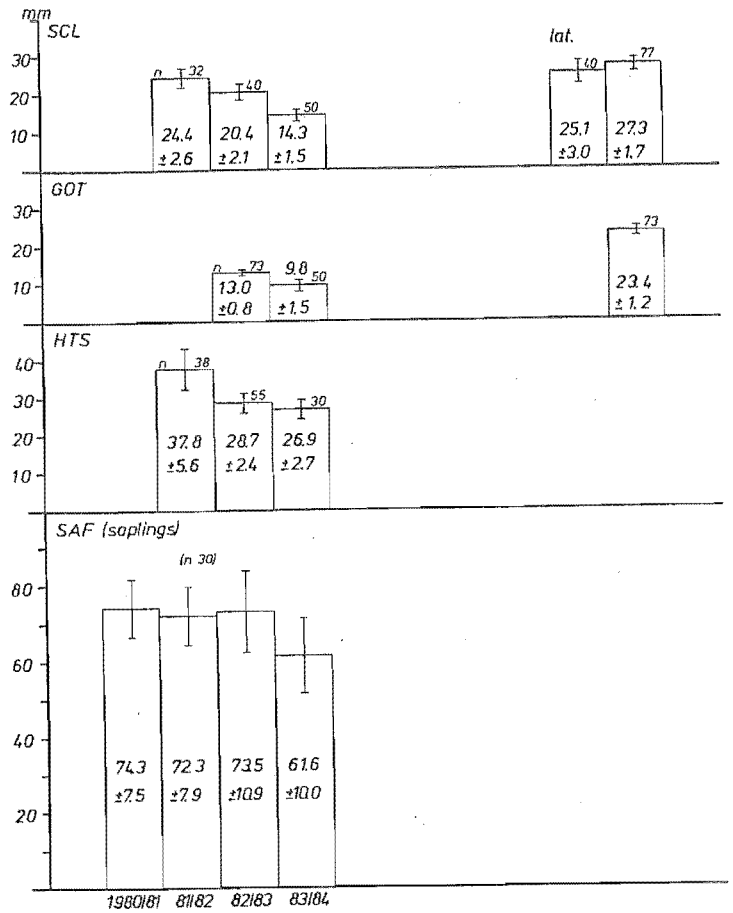

Figure 41. Average annual shoot growth of *Senecio bennettii*.

and limited soil nutrients. A group of overmature shrubs at the forest margin (close to SAF) exhibit a similar growth rate. The scrubline individuals show more extension growth by about 50%, though at a considerably higher altitude. However, they are rooted in a deeper soil and on a N to NW-facing slope which may contribute to better growing conditions. Shrubs in the undergrowth and margins of subalpine low forest were measured at the HTS site and revealed an average annual rate of 31mm extension growth. The highest annual growth of about 70mm was encountered in a group of young saplings less than ten years old growing under a canopy gap at SAF.

No data from other authors concerning growth rates of *Senecio bennettii* seem to be available so far.

(4) *Dracophyllum traversii*

Shoot extension growth of *Dracophyllum traversii* takes place within the funnel-like terminal leaf tuft and cannot be recorded by conventional methods. The same applies for annual shoot length as the species does not develop resting buds of any kind and the leaves, produced at different times of the season, attain the same final size. But if the upper section of the shoot that produces secondary bark for the first time, i.e., four to five years after its own extension growth, is taken to be roughly comparable to the current shoot extension (see section 2 for further explanation), then estimates for annual shoot growth can be given. 138 such measurements from ten shoots of a fallen tree (snowbreak in September, 1983) gave a mean of 14.0± 0.8mm per year. Another collection of ringscars from six trees (107 counts) gave 8.5±0.5mm of shoot extension growth per year. The same procedure applied to saplings at NWS gave a value of 30.9±2.5mm

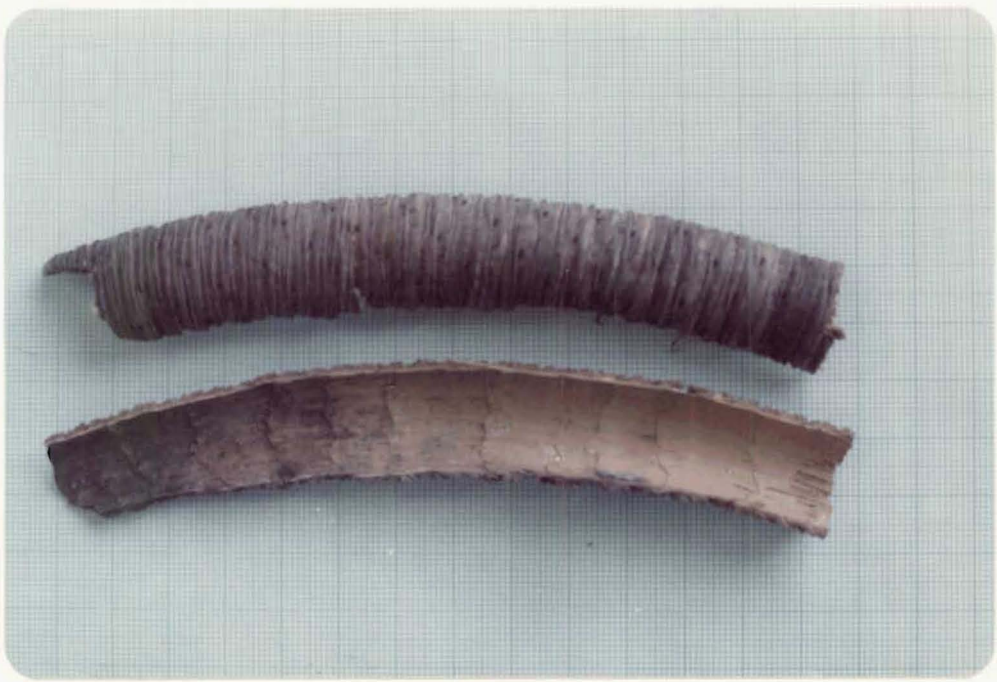

Figure 42. Ringscars (leaf-scars) of *Dracophyllum traversii*

per year. Young individuals produce more leaves per season but internodes are also more extended than in mature trees. In adults, one leaf comes to 1.1mm shoot length whereas in juveniles one leaf occupies 2.5mm shoot length.

The average annual extension growth thus established for mature trees agrees closely with the rate given by Wardle (1960, 1963a), whose calculations were based on ring counts in stem sections.

(5) Summary of shoot extension growth

Table 7: Average annual shoot growth.

	Wardle(1960)	Wardle(1963a)	Bussell(1968)	this study
Hoheria	38mm	65(40-90)mm	60(538*)mm	74(151*)mm
Olearia	152mm	150(100-200)mm	n.d.	27(110*)mm
Senecio	n.d.	n.d.	n.d.	16(70*) mm
Dracophyllum	13mm	10-15mm	n.d.	8-14(31*) mm

* data for large seedlings and saplings

Annual shoot extension growth for adult individuals of all four species concerned proves to be very small. *Hoheria glabrata*, with an average of 74mm per annum, is by far the most productive species of this study, *Olearia ilicifolia* follows with 27mm, and its young shoots are even of a smaller diameter than in *Hoheria*. The shrub *Senecio bennettii* has only 16-25mm annual height growth and for *Dracophyllum traversii* values from 8-14mm were obtained. But it should be considered that the average *Dracophyllum* shoot has an initial diameter of about ten millimetres and will have a higher dry weight per unit length than the other species.

6. LEAF SHAPE AND PHYLLOTAXIS

The typical shape of the leaves of *Hoheria glabrata* is ovate to ovate-lanceolate with a cordate base. The tip is acuminate and usually drawn out to a drip-tip which may be curved to the left or right. The first leaves of the season are usually much smaller and shorter, sometimes having an almost reniform shape. The leaves formed late in the season do not attain full size. Leaves are born singly at the shoot with a pair of lanceolate stipules that are soon shed. A higher symmetry in the arrangement of leaves is not obvious but it could possibly be 5/2, i.e., an angle of 144° exists between the insertion of two successive leaves.

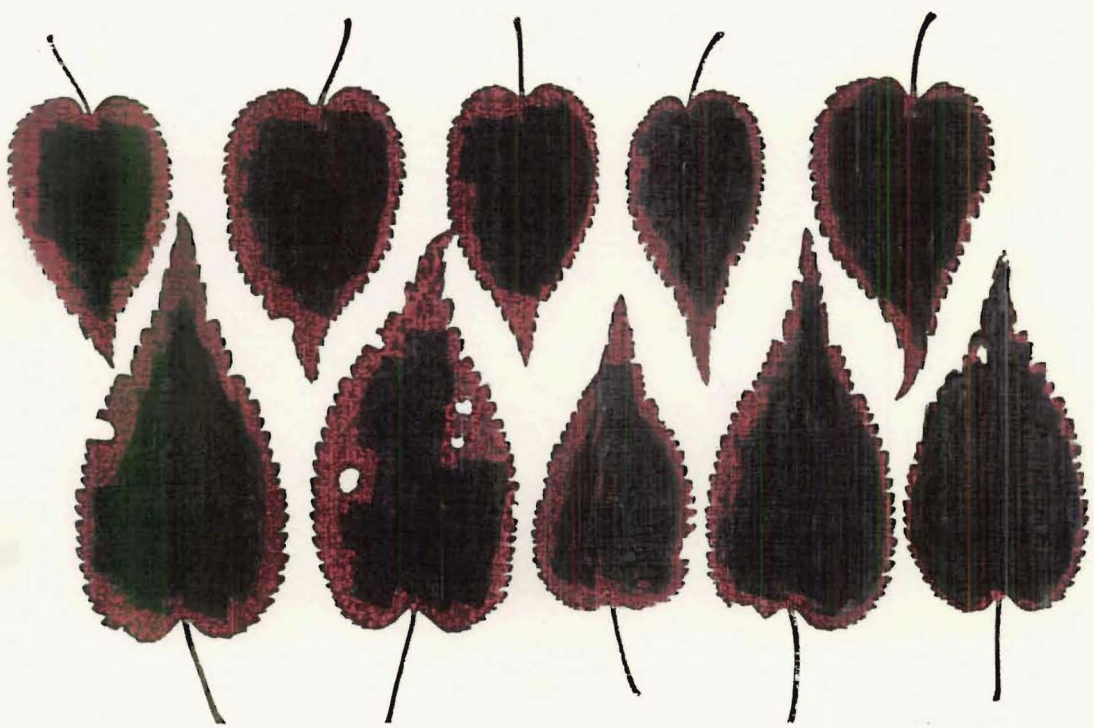

Figure 43. Typical shapes of *Hoheria glabrata* leaves of average size; note curved "drip-tips" (½ natural size).

Olearia ilicifolia clearly reveals a phyllotaxis of 5/2. As usually not more than five full sized leaves per

Figure 44. Apical shoot of *Hoheria* bearing fully grown leaves.

Figure 45. Foliage of *Olearia ilicifolia*; the young expanding leaves of the current season are still clad in a whitish tomentum.

Figure 46. Leaves of *Olearia ilicifolia* (fourth row from left) and its hybrid forms with *Olearia arborescens* (typical leaves in left row) and *Olearia lacunosa* (typical leaves in right row).

Figure 47. Close-up of the foliage of *Senecio bennettii*.

bud are formed each season, mutual shading is kept at a minimum as a result of this arrangement (e.g. Hallé et al, 1978). The leaves become sclerotinized after their extension growth ceases. The last foliage leaf of the season is usually the largest, only to be followed by one subsequently formed scale-like leaf and bud scales.

Senecio bennettii, too, possesses a phyllotaxis of 5/2. This enables the full exposition to sunlight of the usually five full sized leaves per bud that are produced annually. The first leaf of the season is generally much smaller than the subsequent ones and often has a broad-ovate to obtuse shape. The remainder of the leaves increase in size but the younger ones show decreasing size again and the last leaf of the season is only represented by a scale, without a proper lamina.

Dracophyllum traversii has a spiral leaf arrangement which reveals a phyllotaxis of 13/5, i.e., successive leaves share an angle of 138.5°. Again, this symmetry of insertion is correlated with the number of annually produced leaves, a possible provision to keep mutual shading at a minimum. All full grown leaves are equivalent in shape and size.

Table 8: Relationship between phyllotaxis and the number of annually produced leaves per bud.

	phyllotaxis	leaves per bud
Hoheria	5/2 ?	8-12
Olearia	5/2	5 + scales
Senecio	5/2	5 + scale
Dracophyllum	13/5	12-14

Figure 48. Phyllotaxis in *Senecio bennettii*, the sixth leaf (scale-leaf only) has the same orientation as the first leaf.

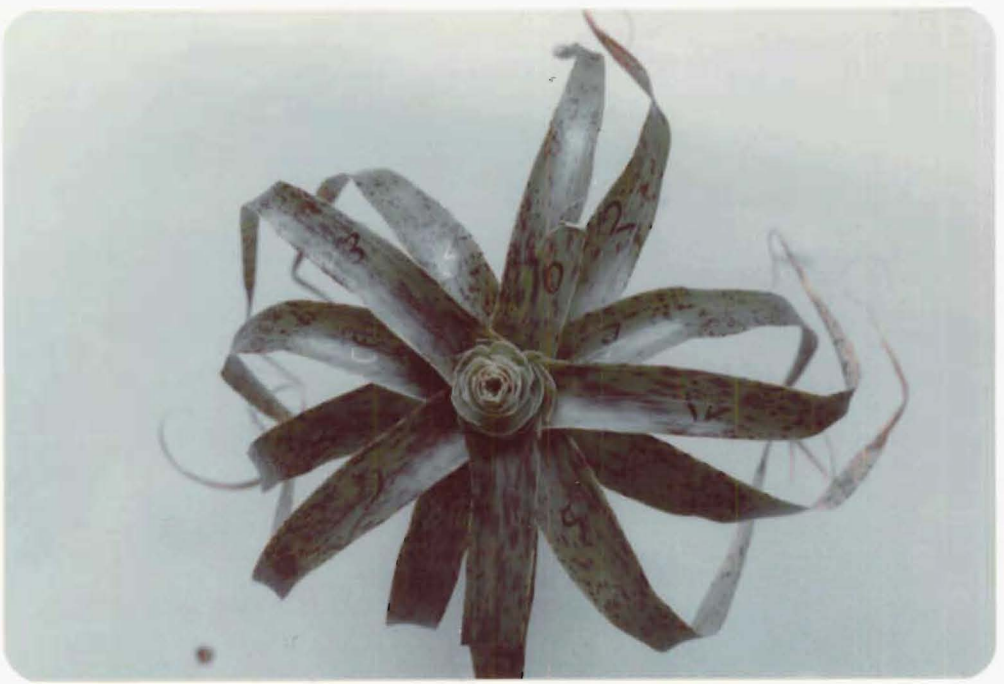

Figure 49. Phyllotaxis in *Dracophyllum traversii*, leaf 1 (pointing downwards) and leaf 14 (partly cut off) conincide in their position at the shoot.

7. LEAF AREA GROWTH, LEAF PERSISTENCE AND LITTERFALL

(1) *Hoheria glabrata*

Leaf production in *Hoheria glabrata* begins with the unfolding of the first leaf from the overwintered terminal bud. This occurred during the 3rd and 4th week of October, 1982, and during the 4th week of September to the first week of October in 1983, i.e., three weeks earlier. Swelling of the buds could already be observed during the first October week in 1982, and during the 2nd September week in 1983, two weeks before the actual bud break. In 1982/83, leaves were counted at the stands HGF and GOT. The number of leaves per apical shoot (equivalent to the present leaf area) peaked in late January with 10.5 at HGF and 8.4 leaves per shoot at GOT, but production of new leaves continued until mid February when older foliage was already being shed. Altogether, 12.6 leaves per shoot were produced at HGF and 9.3 at GOT during the whole season. The trees were bare in early May. A more complete study was made during 1983/84, when trees at the stands PLC, GOT and APS were investigated (figure 51). Maximum numbers of leaves per shoot were present in mid December at GOT and in late December at both other stands. No new leaves were produced after mid December at GOT and PLC, and about mid January at APS. Total numbers of leaf production per shoot were 8.6 (GOT), 9.9 (PLC), and 12.7 (APS). The trees at APS kept the maximum amount of foliage later in the season (mid December to mid February) than the other two stands (mid November to mid January), and shedding of leaves was therefore rather accelerated compared with GOT and PLC. All leaves were shed by 31st of May or slightly earlier.

Figure 50. Expanding foliage of *Hoheria glabrata* early in the season; the lanceolate stipules are still attached.

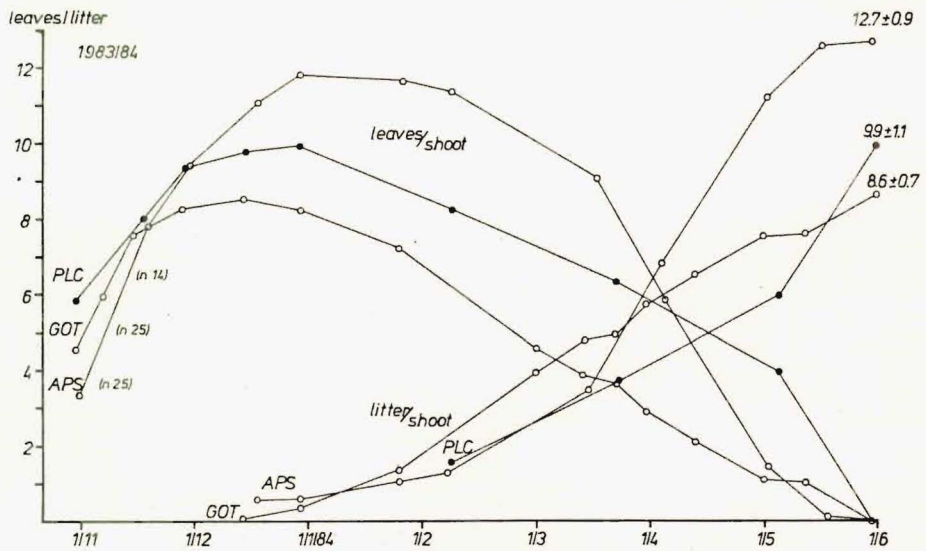

Figure 51. Seasonal variation in the number of leaves per shoot and litter production in three stands of *H. glabrata*.

In two cases - GOT and APS - estimates for seasonal leaf area growth were attempted (figure 52). The graphs closely resemble the previous curve, the only difference is the steeper gradient at the beginning of the season, where each leaf, when simply counted, has the same value on the scale, but small young leaves naturally have less area when

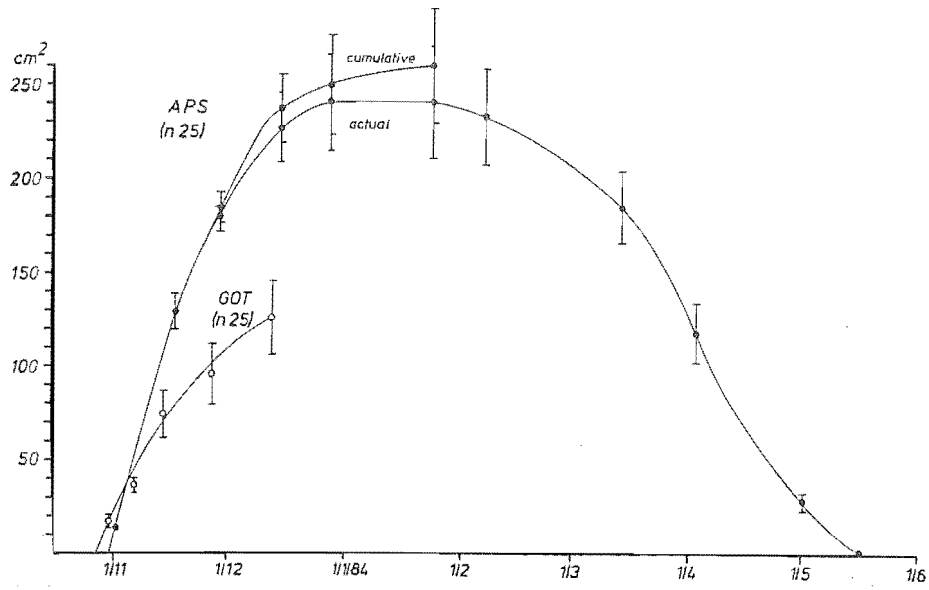

Figure 52. Seasonal leaf area increment in *Hoheria glabrata*.

leaf area development is considered. Maximum leaf area per shoot was estimated at 126.5cm^2 at GOT and at 241.4cm^2 at APS. Production of total leaf area per shoot coincided with the first value at GOT but was slightly higher at APS (260.4cm^2).

Though *Hoheria glabrata* may bear foliage for up to nine months (September to May), the individual leaf remains on the tree for a period of 3-5 months only. The first leaves were shed in mid December, 1983 (probably later than that during the 1982/83 season) and litterfall became more evident by mid February. But early shedding was restricted to the older, lower leaves only. In the three observed seasons from 1981/82 to 1983/84, *Hoheria glabrata* foliage turned conspicuously yellow about mid April and shedding continued until mid to late May. Below average temperatures in the 1982/83 season seem to have caused a slightly earlier litterfall but no exact records of individual trees were made.

(2) *Olearia ilicifolia*

Swelling of apical buds of *Olearia ilicifolia* was

first noticed on October 1st, 1982, but already during mid September, 1983. Bud break was about 3-4 weeks later and it took another fortnight for the first leaf to unfold. This took place during the 2nd week of November, 1982, and the last week of October, 1983. Lateral buds generally needed another fortnight to develop first foliage. Continuous measurement of leaf length, that was later converted into leaf area data, was carried out at trees at OTR and PLC (figure 53). Initial growth of leaves is rather slow but maximum leaf area increment is attained 2-3 weeks after unfolding of

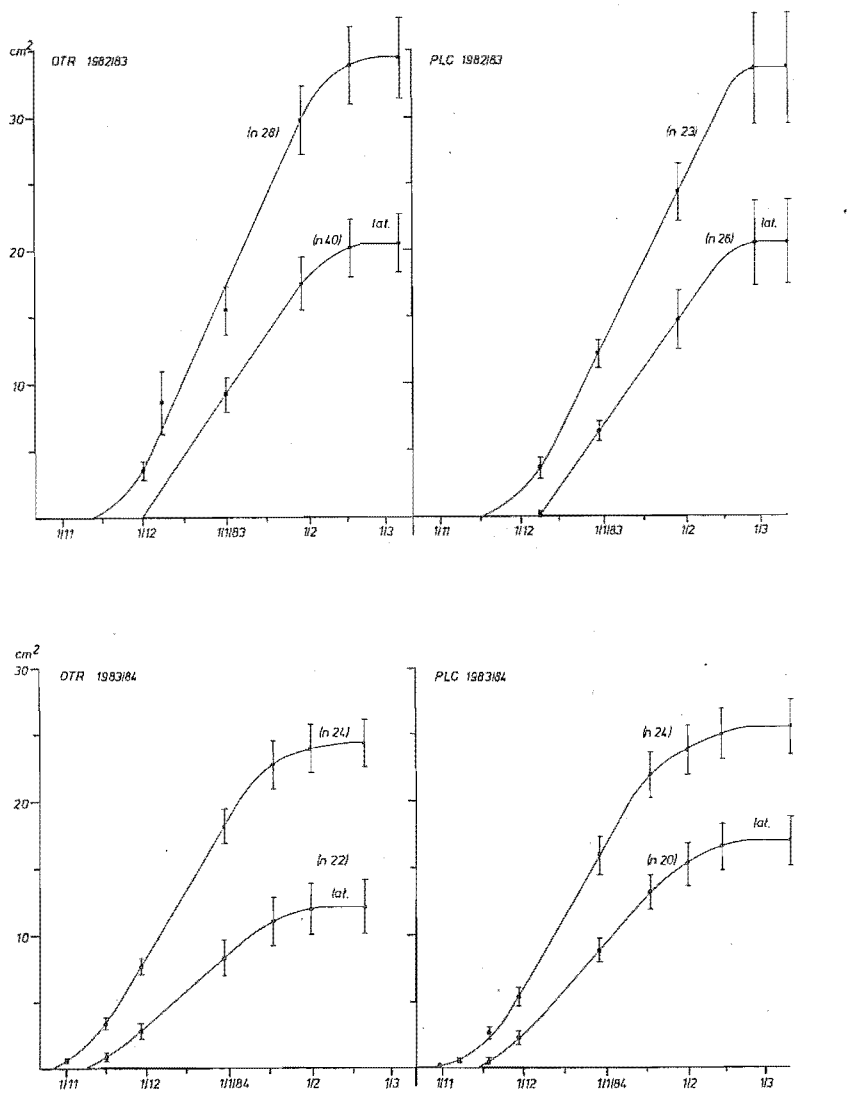

Figure 53. Seasonal leaf area increment of apical and lateral shoots of *Olearia ilicifolia*.

the first leaves, amounting to 34-35mm^2/d for the apical, and 18-23mm^2/d for the lateral shoots in the 1983/84 season, and to 41-44mm^2/d and 28-29mm^2/d, respectively, during 1982/83. This phase of maximum growth lasted for 60 (to 70) days in 1982/83 (1st of December to January/February) and for only about 50 days in 1983/84 (20th of November to 5th-10th of January). Growth rates declined thereafter and leaf area growth ceased during the last week of February, 1983, and within the 3rd week of the same month in 1984. The total period of leaf area growth was therefore about one week longer during the 1983/84 season, but the period of maximum growth was at least ten days shorter in 1983/84 and maximum daily increment rates were much reduced, too. Total new leaf area was thus condsiderably lower than the previous season.

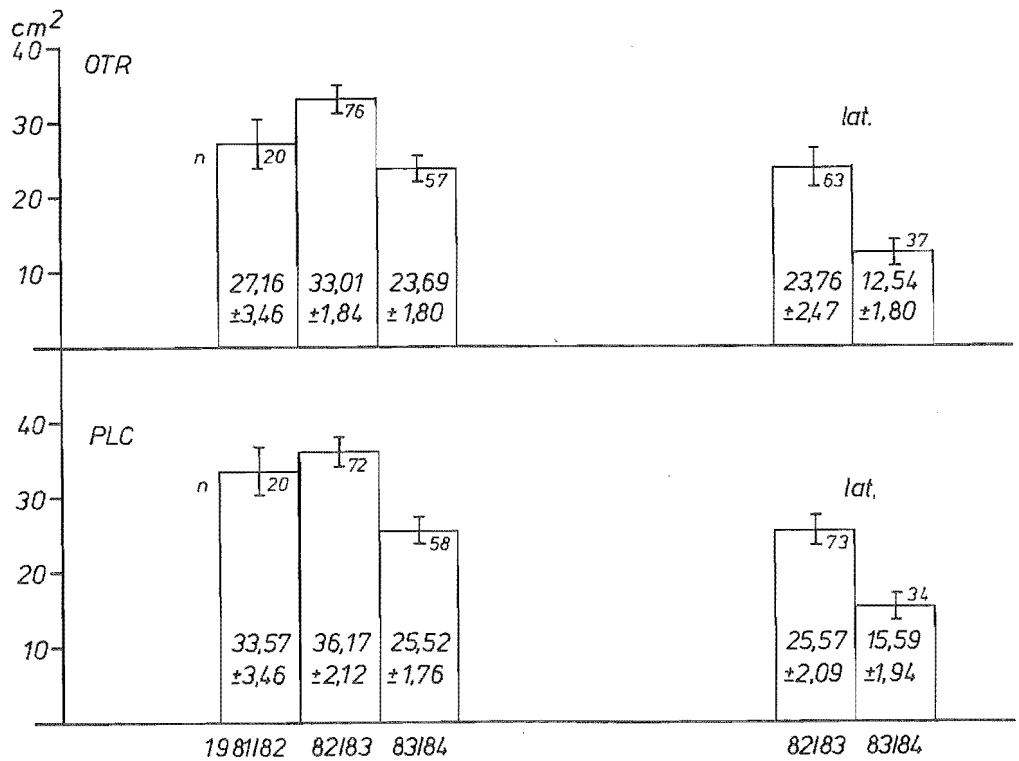

Figure 54. Average annual leaf area per shoot in *Olearia*.

After more extensive sampling, figures for annual leaf area production per shoot were established for the last three seasons (figure 54). The 1983/84 production was in fact only 71-72% of the 1982/83 figure, and even less (53-61%) when lateral shoots are compared. The 1982/83 leaf area production also proved to be about 10-20% above the 1981/82 figure which is quite unexpected when compared with the general trend of biomass production during the last three seasons. The leaf area of lateral branches is, in all four cases, about 10cm^2 lower than the production of the respective apical shoots.

When annual foliage production is expressed as average number of leaves per shoot these relationships are confirmed.

Table 9: Average number of leaves per terminal shoot and mean area of individual leaves in *Olearia ilicifolia*.

	(OTR) 1981/82	1982/83	1983/84	(PLC) 1981/82	1982/83	1983/84
leaves	5.40	6.24	5.29	6.16	6.62	5.46
mm^2/leaf	503	529	448	545	546	467

The average area for one individual leaf (mean of leaf area divided by the mean number of leaves per shoot) shows that during the 1983/84 season not only fewer but also smaller leaves were produced. Leaves at stand PLC were generally slightly larger than at OTR.

The total number of leaves per shoot, i.e., currently produced new foliage plus the remaining older leaves of the previous season, is shown in figure 55. The maximum of 10.4 leaves at PLC is reached at the end of January, at OTR this maximum is depressed to only 8.85 leaves per shoot in mid February owing to an accelerated leaf shedding during December and January. Relationships between litter production

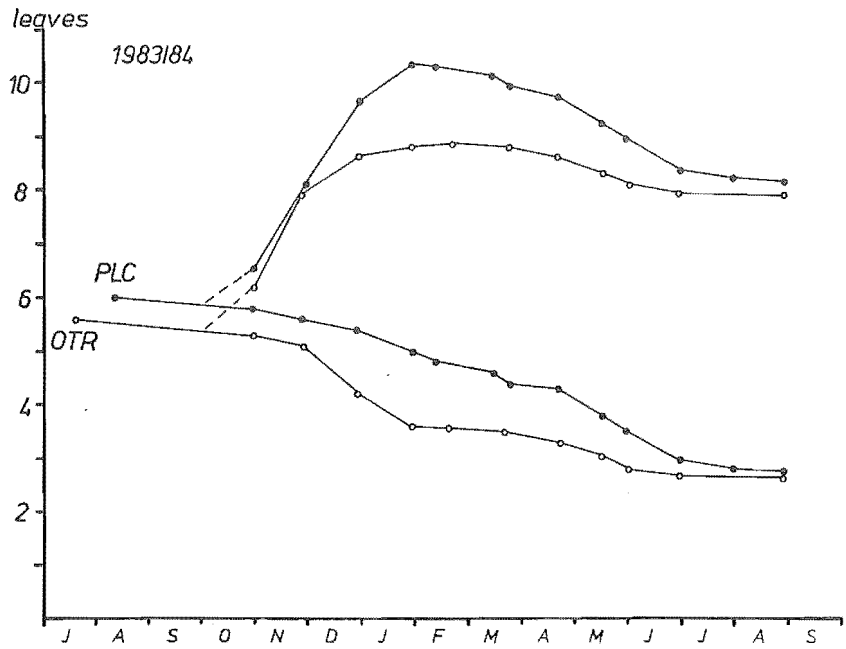

Figure 55. Seasonal variation in the total number of leaves per shoot; the lower curves represent the remaining older leaves that were produced in the previous season.

and new leaf area growth becomes still more apparent when the number of remaining older leaves per shoot is directly compared with current leaf area growth (figure 56). Though the data for the 1982/83 season are scanty it is obvious that litterfall is accelerated during the time of maximum leaf area growth from December to late February. This cycle is repeated in 1983/84 at OTR lasting from about mid November to late January/early February; litterfall decreased thereafter and stopped in late June. The mentioned relationship was, however, less pronounced at PLC where litter production increased only slightly from November onwards but continued at about the same rate until early July when it came to a standstill. It may be supposed that nutrient reserves are withdrawn from the old foliage during the period of maximum growth of the new leaves. It is possibly more pronounced at OTR because soil nitrogen is in shorter supply in the rela-

tively young soil but is more readily available at PLC. As comparatively little new foliage was produced in 1983/84, litterfall was not particularly accelerated and part of the 1982/83 foliage was kept during the winter of 1984.

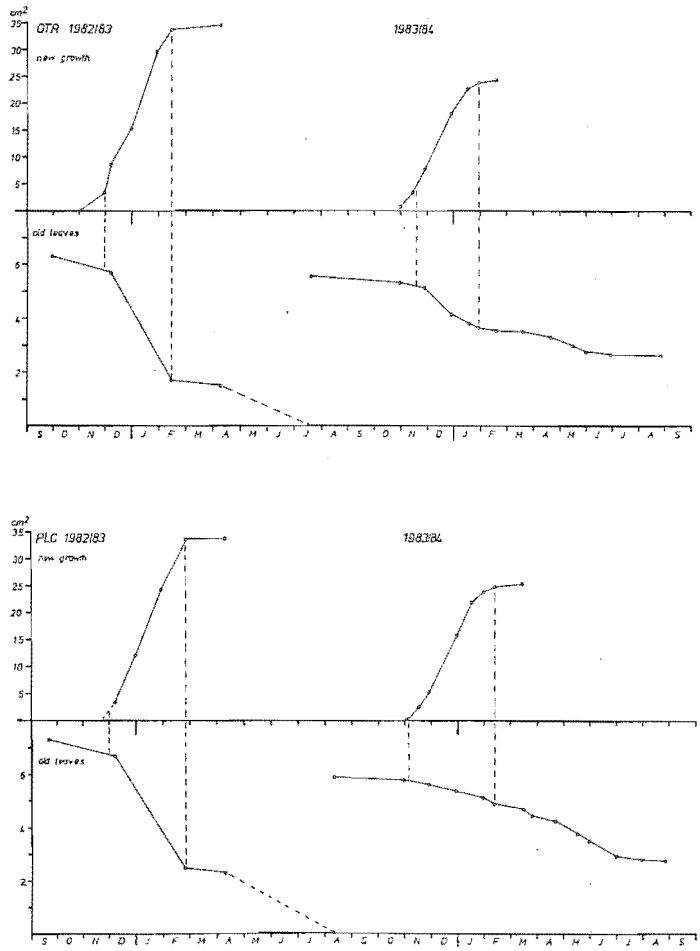

Figure 56. Relationship between seasonal leaf area growth and litterfall in *Olearia ilicifolia*.

Foliage of *Olearia ilicifolia* remains on the tree for about one year. Most of the leaves that grow during November and December will be shed in December to January of the following season, thus giving a mean age of 12-14 months. When a season with considerably lower production occurs, as in 1983/84, part of the previous season's foliage may remain on the tree for a longer time, i.e., until the beginning of the

third growing season. In some cases, the smallest leaf - the first one to unfold in the growing season - is already shed during March to May of the current season thus attaining an age of only 6-8 months. Wardle (1963a) also estimated a leaf persistence of about one year for *Olearia ilicifolia*.

(3) *Senecio bennettii*

Senecio bennettii starts its growth considerably later in the season than both *Hoheria* and *Olearia*. It was not before the 2nd week of November, 1982, that swelling of the buds was noticeable but subsequent progress was slow; bud break occurred during the first week of December and it took until the second half of the month for the first leaf to unfold. Bud swelling was already in progress during the second half of October, 1983, with shrubs and seedlings in the undergrowth of subalpine forest starting as early as late September. Bud break was in mid November and the first leaf unfolded in late November.

Continuous observations of leaf area increment were made for the stands GOT and SCL (figure 57). Maximum growth rates for apical shoots of $92mm^2/d$ (GOT) and $95mm^2/d$ (SCL) were maintained from the 4th week of December until the 1st week of March, 1983, production then gradually declined and came to a standstill in the last week of April. Leaf area growth started about two weeks later for lateral buds and was considerably slower (maximum rate $34mm^2/d$) compared with apical shoots. There was a lag of about one week between the start of leaf area growth at GOT and SCL.

Leaf growth began about three weeks earlier in 1983. The period of maximum increment growth lasted from the 4th week of December to the 2nd week of February, i.e., three

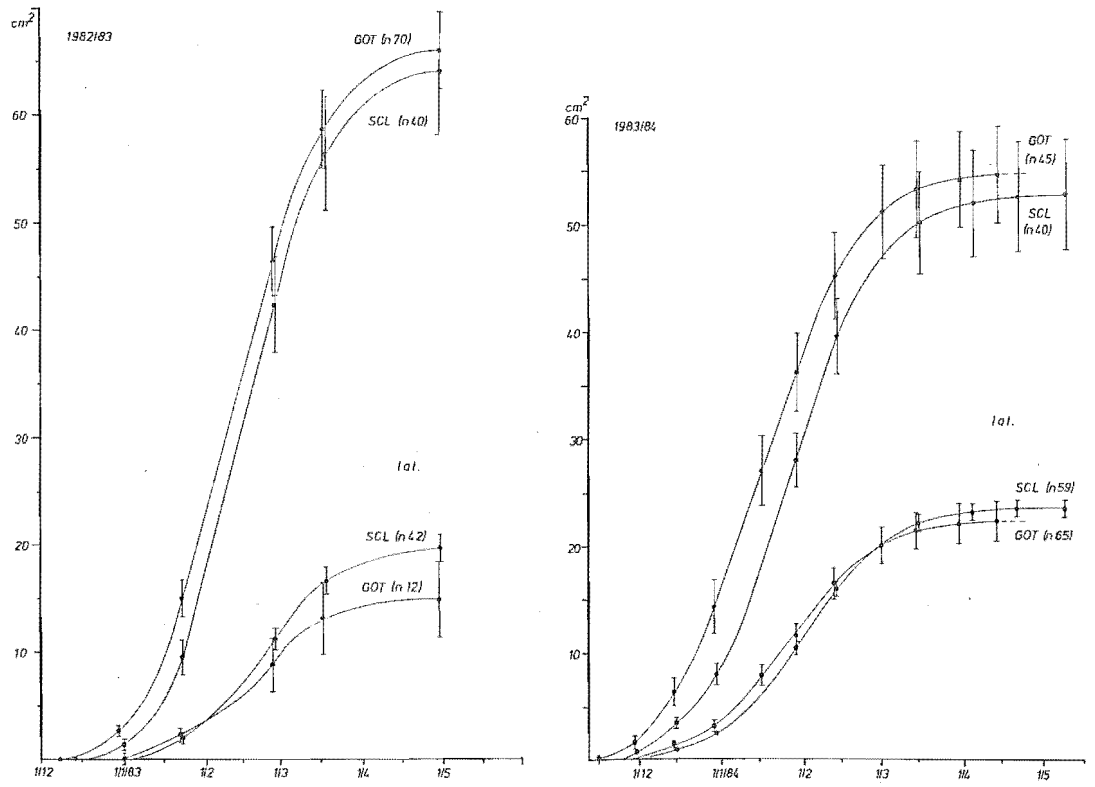

Figure 57. Seasonal leaf area increment in apical and lateral shoots of *Senecio bennettii*.

weeks less than during the previous season (seven weeks compared to ten), and daily rates were only 70.5mm^2/d (GOT) and 74mm^2/d (SCL). Growth ceased completely during the last week of April. Leaf area growth of lateral shoots was with 37mm^2/d comparable to that of the previous season.

Figures for average annual leaf area production since 1981/82 are given in figure 58. Data for apical shoots show a considerable decrease from 1981/82 to 1982/83 when only about 85% of the previous season's leaf area was produced, and a further decrease to 1983/84 when only 83% of the 1982/83 area (or 68% of 1981/82) was attained. The reverse seems to apply when leaf area of lateral shoots is considered. Virtually no lateral shoots were produced in 1981/82, so no figures are avialable, but the mean area for 1983/84 is clearly above the 1982/83 figure; the difference of the means

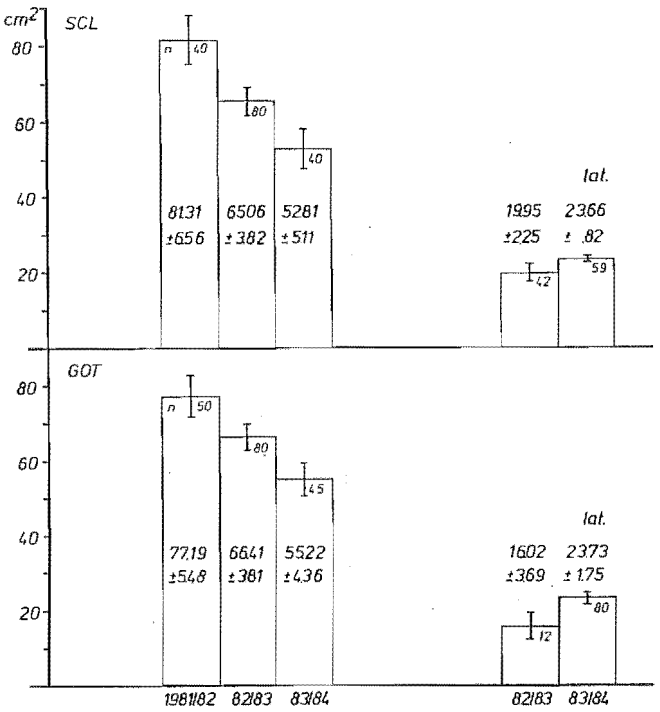

Figure 58. Average annual leaf area per shoot in *Senecio*.

at the SCL stand is significant at the 2% level.

When the average number of leaves per shoot is determined a similar result is obtained, but the mean size of individual leaves shows only a slight decrease (table 10).

Table 10: Average number of leaves per shoot and mean area of individual leaves in four stands of *Senecio bennettii*.

	GOT	SCL	SAF	HTS	
1981/82	7.18±0.27	7.00±0.18	6.76±0.32	7.14±0.64	leaves
	1075	1162	1092	1650	mm^2
1982/83	6.45±0.23	6.90±0.18	6.31±0.30	6.72±0.28	leaves
	1030	926	997	1559	mm^2
1983/84	5.70±0.24	5.62±0.18	n.d.	n.d.	leaves
	967	940			mm^2

The total number of leaves per apical shoot throughout the season is shown in figure 59. The maximum occurred in mid March, 1983, (13.0 at GOT), but in mid February, 1984,

(12.9 leaves per shoot at GOT) because of the earlier start of the growing season.

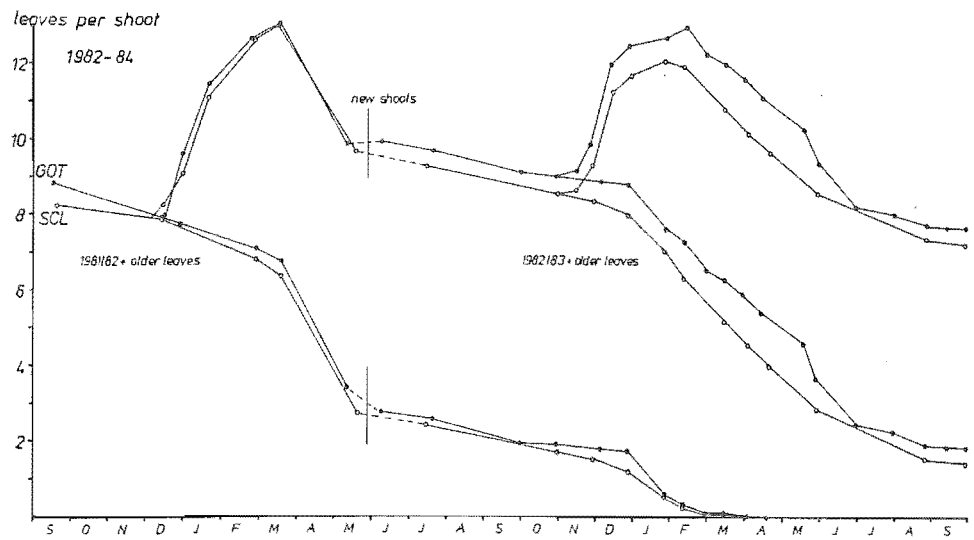

Figure 59. Seasonal variation in the total number of leaves per shoot in *Senecio bennettii*.

Old foliage leaves are shed throughout the year, though at a very much reduced rate during winter to early summer. In the 1982/83 season shedding of old leaves only accelerated by early to mid March, after the new leaf area growth was almost completed, and lasted until late May. Litterfall increased again in late December, 1983; this time the date coincided with the start of maximum leaf area growth of the new foliage. Leaves continued to be shed at this higher rate until the end of June. The lower rate of litterfall from July onwards will be at least partly due to the fact that an increasing number of shoots had by then already lost all of their older foliage and shedding of the 1983/84 leaves will not commence until new growth starts late in 1984. It is therefore assumed that shedding of leaves, and thus physiological activity, continued throughout the winter of 1984,

which was evidently a very mild one. Litterfall came almost to a standstill in September and October, 1984. The starting dates of maximum litterfall differ by about ten weeks between the two seasons, only three to four of which can be accounted for by the earlier start of the growing season in 1983/84.

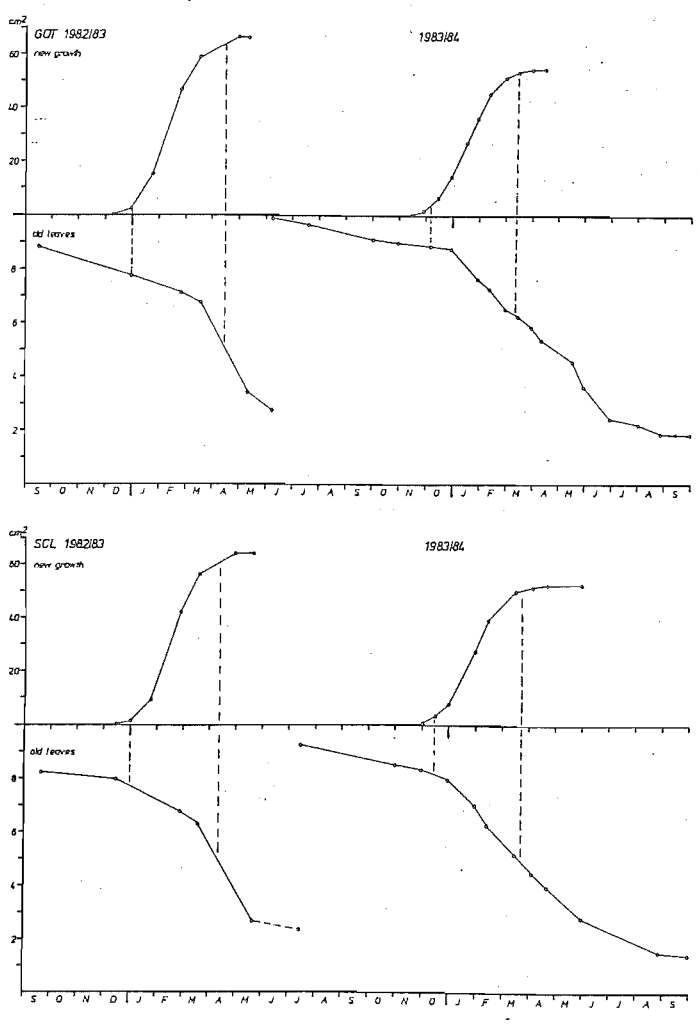

Figure 60. Relationship between seasonal leaf area growth and litterfall in *Senecio bennettii*.

The average life expectancy of *Senecio bennettii* leaves is estimated at 16-18 months but it strongly depends on whether the individual leaf is formed early or late in the season. Leaves growing from November to January will usually be shed late in the following season reaching an age

of 15-16 months, but leaves formed in February/March may survive until the beginning of the subsequent season thus attaining 18-22 months. During the earlier months of the growing period, leaves of three seasons can always be seen together on the same shoot, in some cases all leaves of the last season are shed by March/April giving a minimum age of about 11-13 months. In May, 1983, one harvested shoot was still bearing three complete leaf cohorts dating back to at least December, 1980, thus giving a maximum age of 30 months. Wardle's estimate of one to two years is well within these limits (Wardle, 1963a).

(4) *Dracophyllum traversii*

Dracophyllum traversii has the most extended growing season of the four species under consideration. Leaf length measurements were started in early October, 1982, but it was revealed that growth had already progressed by this time, possibly since the last week of September. Leaf growth lasted until late April, 1983. Measurements for the following season were therefore already carried out from mid August for saplings and from early September for mature trees. Growth ceased in the first week of May, 1984, i.e., the complete growing season lasted for 8-8½ months, compared with 6½-7 months in 1982/83 which was an extremely cool and wet summer.

Though leaf length can be conveniently measured, a conversion of the data into leaf area growth can only be attempted for a model shoot based on a wide range of individual measurements. Calculations for individual shoots or even trees would require extensive sampling and data processing procedures. Seven complete shoots were harvested to determine the length and area of the lamina of each single

leaf. Results were plotted on graph paper revealing the length - area relationship of leaf growth. Other data concerning the model shoot were obtained throughout the field study. After transformation into leaf area values the data given in table 12 are obtained.

Table 11: Mean figures for the dimension of the model shoots.

stand	number of leaves total/growing/mature			mean length	annual incr.	new l. p/a	difference in length*
NWS	105±9	46	59	589±12mm	225mm	18±2	13mm
SAF	81±7	43	38	498±7mm	160mm	14	12mm
HTS	74±5	41	33	446±5mm	129mm	13	11mm

*of successively formed leaves.

Table 12: Leaf area of the model shoots.

stand	area per shoot total	growing	mature	leaf size	annual addition
NWS	7018.3	1364.9	5653.4	95.82	1649.1cm^2
SAF	3544.3	813.5	2730.8	70.02	935.3cm^2
HTS	2413.5	588.6	1824.9	55.30	651.8cm^2

Of the seven complete shoots used for estimating the leaf length - leaf area relationship, four, all sampled at HTS, were considered for determination of their actual total leaf area. This gave a mean figure of 2420.7cm^2 (table 13).

Table 13: Mean leaf area per shoot as determined from samples.

shoot	1	2261.7cm^2
"	2	2848.0cm^2
"	3	1723.3cm^2
"	4	2849.7cm^2
	$\bar{x}$	2420.7cm^2

This leaf area figure agrees quite closely with the mean area calculated for the model shoot for HTS (2413.5cm^2). Thus the

mean total leaf area determined from only four sample shoots proves to be comparable with the established model. It can therefore be safely assumed that the calculated model shoots are in fact a good representation of the actual mode of leaf area growth. The results of the seasonal leaf area increment that were calculated on this assumption from leaf length measurements are shown in figure 61. Maximum daily growth took place during the period from 15th-18th of October to 10th-13th of March, i.e., about 150 days. The actual readings for mid and late December, 1983, are situated below the graph because the marked leaves were approaching maturity and rates declined slightly; new younger leaves were measured later on.

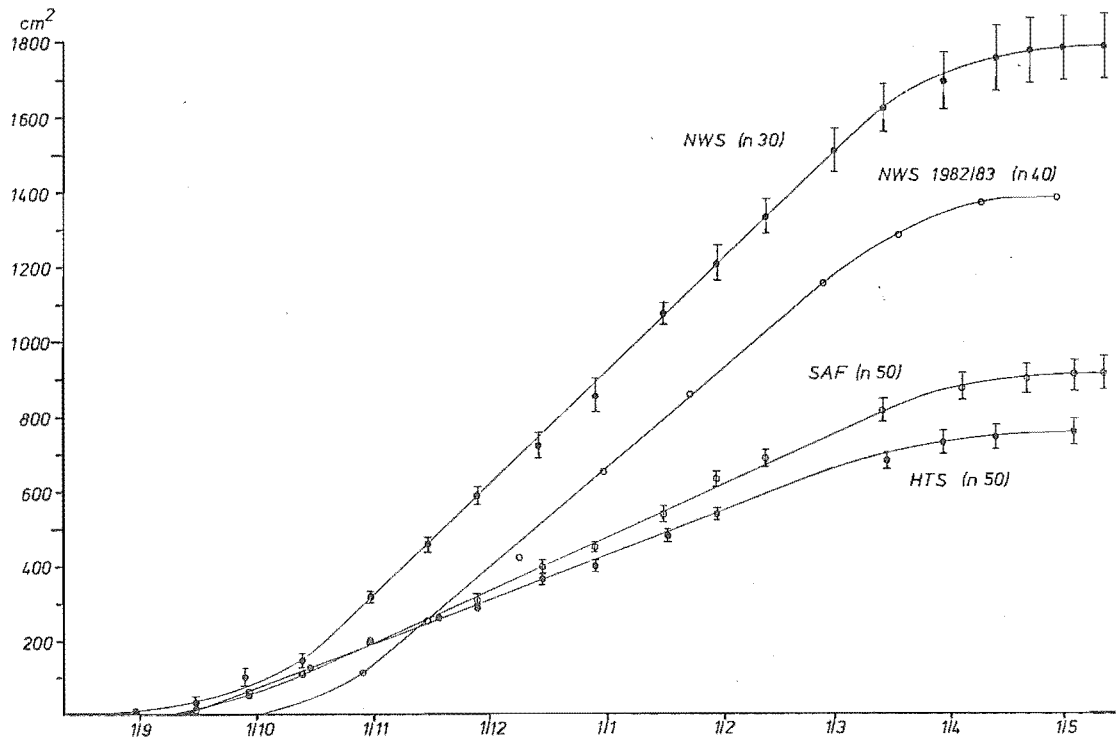

Figure 61. Seasonal leaf area increment in three stands of *Dracophyllum traversii* during the season of 1983/84.

In all three monitored stands growth rates were highest in the saplings at NWS showing an average increment of 9.71cm^2/d.

Daily increment was considerably lower at SAF (4.58cm^2/d) and HTS (3.85cm^2/d). In 1982/83, the respective period of maximum growth was only 130 days (end October to beginning of March) and the average daily rates were 8.58cm^2/d at NWS.

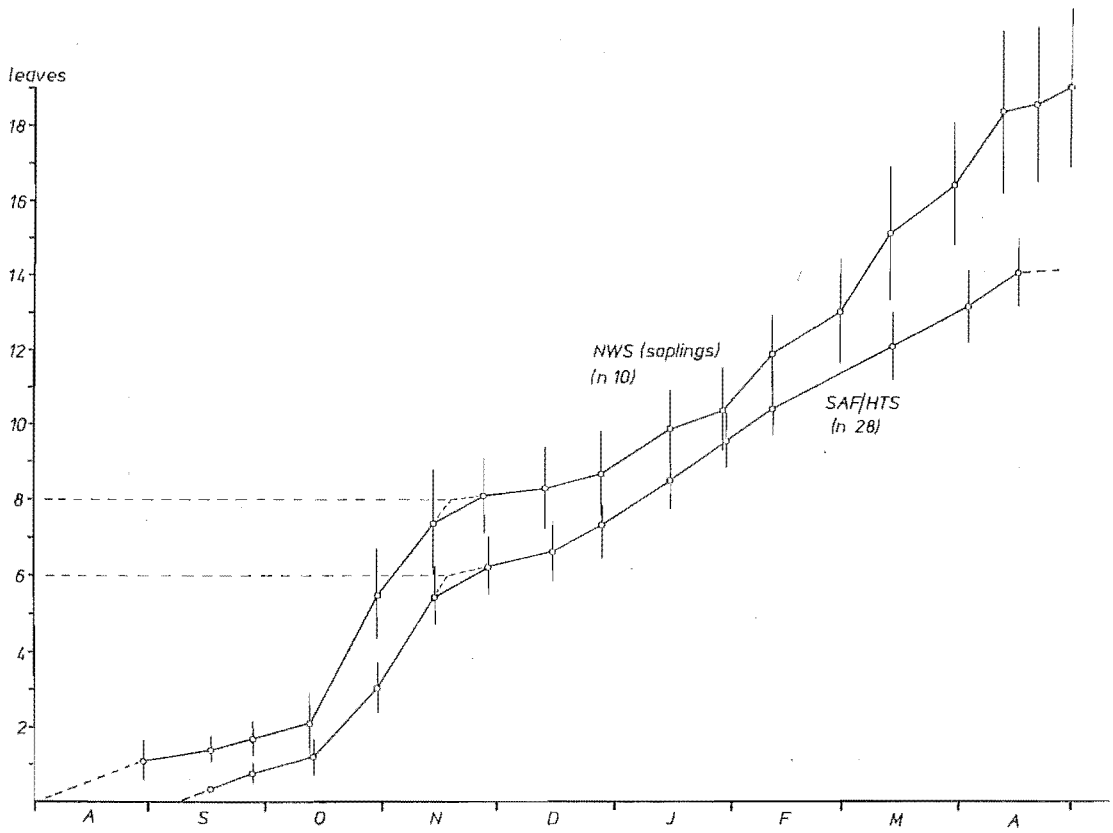

Figure 62. Seasonal production of new leaves in *Dr. traversii*.

An average of 14 new leaves per shoot were produced in 1983/84 with even more, 18-19 per shoot, in the saplings at NWS. The rate of production does not seem to be correlated with overall area growth but reveals an independent rhythm which is repeated in both saplings and adult trees (figure 62). The first new leaf of saplings must have been formed already in early August when area growth was not detectable. Probably, growth activity starts at the tip of the shoot apex and moves down to the older leaves. There was a notable acceleration of new leaf production from mid October to late

November, followed by a period of slowing down until mid December. Thereafter, the rate of production was uniform in adults and more or less steady in saplings, but this may be due to the small sample size (n=10) in the latter. Remarkably, the abrupt decrease in new leaf production occurs exactly at eight leaves for saplings and six leaves for adults. It is therefore assumed that not all small young leaves were counted initially, but that some, i.e., eight or six, respectively, were hidden deep inside the funnel-like terminal tuft of leaves. These young leaves would emerge relatively fast once environmental conditions are suitable but then there would be an apparent lag in leaf emergence because the newly formed leaves of the current season will need some more time to become visible to the observer. Sectioning of some shoots later on revealed that between six to nine leaf initials can usually not be counted under natural conditions.

A total of 14±0.9 new leaves was produced during the 1983/84 season. Given the mean annual extension growth of 130-160mm, the leaves formed early in the season may reach their final length late in the third, but more probably early in the fourth growing season. Leaves formed later in the year will only cease growth early in their fifth season. By the time a leaf has attained its final length it will be about 3½ years old. Leaves of saplings may need only 2½ seasons to grow to final length. These results are in absolute contrast to Wardle's statement on leaf growth and longevity of *Dracophyllum traversii* foliage (Wardle, 1963a, p.35). Though it is understood that growth will be enhanced in warmer environments, i.e., lower altitudes, it is hard to imagine

any leaf growing from primordial length to 60cm in one year under natural conditions. When the total number of leaves per shoot was determined it was found that 41-43 younger leaves had not yet attained their final length. If 14 new leaves are formed annually, the last group of these younger ones would be in their third year and most of them would continue to grow in the subsequent fourth season. Moreover, another 36 fully grown leaves are also present at the same shoot adding a further 2½ seasons which brings the average period of leaf persistence to 5-6 years. Wardle stated that leaves persisted for 3 years after full length was attained (Wardle, 1963a).

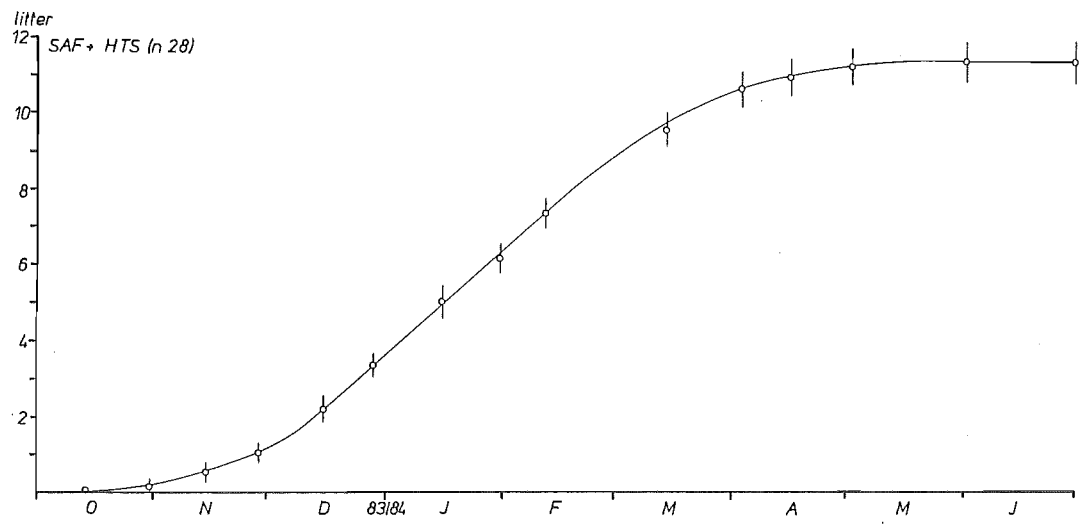

Figure 63. Seasonal cycle of litterfall in *Dr. traversii*.

Litter production is closely correlated with current leaf area growth (figure 63), but there is a lag of about four weeks between the start of leaf growth and litter production. The same lag is again noticeable when the dates of maximum area growth and litterfall are compared. This lag is to be expected because the old leaves will still remain on the tree for some time after most of their metabolites

have been transferred to other tissues and will only be shed after the necessary separation layers are fully developed. The complete period of litterfall in 1983/84 extended from mid October to the beginning to mid May. No litter was shed during the winter months.

8. BUD FORMATION AND PROTECTION OF THE RESTING SHOOT APEX

Most woody plants of the temperate zone or otherwise seasonal climates form specialized resting buds at the end of each growing season. In areas with severe winters these buds are enveloped by a number of protective structures, usually modified leaves. In the southern temperate zone, these features are generally less prominent and more or less unprotected shoot apices occur as well.

Both *Hoheria* and *Olearia* have specialized resting buds. The buds are formed when the shoot growth ceases. *Hoheria glabrata* forms a large apical bud at the apex of terminal shoots as well as smaller lateral buds in the axils of the leaves. The buds are protected by stipules with tomentose surfaces and additional varnish excretions and, according to Wardle (1963a), by additional abortive foliage leaves. Bussell (1968, p.69) states that formation of the new resting buds of several native species (*Hoheria glabrata, Fuchsia excorticata, Aristotelia serrata)* commences immediately after the previous buds have opened. New leaf primordia can be found after three weeks and the bud is completed after six weeks in *Hoheria glabrata*, containing between 6-10 leaf primordia (Bussell, 1968a).

The resting bud of *Olearia ilicifolia* is protected by two or three scale leaves and to some extent by the grooved

petioles and the sheath like leaf bases of the two youngest foliage leaves. Axillary buds are completely covered by the base of their axillant leaf but are as a rule abortive, except for the one, two, or sometimes three uppermost buds. Only in young, fast growing individuals up to four or five axillary buds may develop into sidebranches.

Senecio bennettii has unspecialized buds (to apply Wardle's terminology) but the shoot apex remains invisible during the resting period and seems sufficiently protected by the densely packed leaf bases of the upper leaves. As it appears, only the uppermost one or two small, or scale-like leaves, form axillary buds that produce lateral branches; one or two further lateral branches may arise from the axils of the first leaves of the new growing season.

The shoot apex of *Dracophyllum traversii* survives the winter without any additional protective structures. The spirally arranged and tightly packed leaves close up above the apex, making it externally invisible and provide sufficient insulation from the environmental conditions. Leaf growth and cell division, however, cease during the resting period.

9. MORPHOLOGY AND TIMING OF FLOWERING

(1) *Hoheria glabrata*

Flowers are born laterally in this species. Allan (1961, p.343) states that there are "*Flowers ... in cymose fascicles of 2-5 or solitary...*" but in the Arthur's Pass specimens, flowers were only born in clusters of three unless the number was diminished by abortion of individual flower buds. The triple cluster appears to be fixed morpho-

logically as the individual vascular bundles of the flower petioles are derivatives of the ternate leaf trace visible after abscission. The primordial axillary buds can alternatively form resting buds and possibly develop sidebranches during the next season, or switch to the growth of reproductive structures, i.e., three flower buds, during the current season. It is not known whether this alternative is predetermined at bud formation or may be influenced by the environmental conditions during the early growing season. Trees in full bloom bear flowers in all but the uppermost one or two leaf axils of the current season's shoot. The remaining axillary buds will overwinter and give rise to lateral branches in the following season. Allan (1961) says that the flowering season is November to January, but this may be true for lower altitudes only. At Arthur's Pass flowering lasted from about mid February to mid March, 1982, and almost all trees were in bloom. After the cold and wet 1982/83 summer, however, the timing was different and only very few flowers were seen from mid March to almost mid April. Though flower buds were noticed after mid January, most of these soon aborted. Not a single *Hoheria* seed was to be found in the investigation area, the nearest seed bearing trees were located south of Halpin Creek at an altitude of 700m. In the subsequent 1983/84 season the first flower buds opened on February 9th at Pegleg Flat (830m), and on February 20th at the APS stand (915m). Flowering lasted until mid March and resulted in a good seed crop. It is presumed that both 1981/82 and 1983/84 represented normal seasons giving good seed crops and that only particularly cold and wet summers will tend to reduce flowering and seed production. An average leading

shoot can bear up to 30 flowers and may produce as much as 450 seeds, most of which will be viable.

Figure 64. Flowering shoot of *Hoheria glabrata*.

(2) *Olearia ilicifolia*

Flowers are born in capitula in large corymbs. The corymbs arise from the uppermost resting buds in the axils of foliage leaves. Usually only one corymb is produced per shoot but two or three may also be formed in some cases.

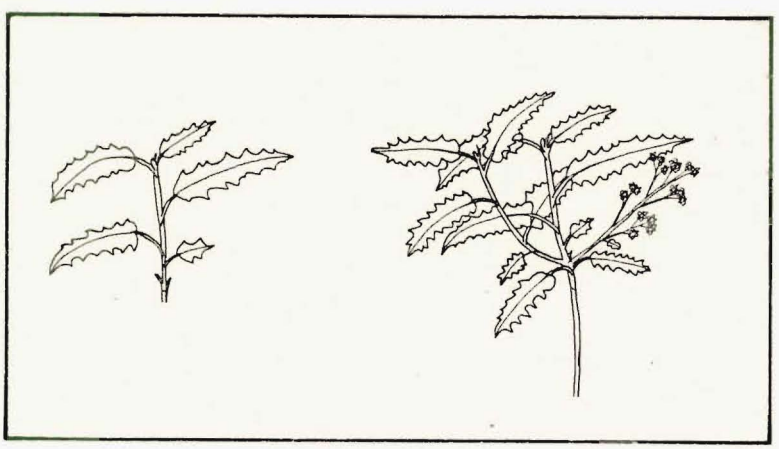

Figure 65. Morphology of a flowering shoot of *O. ilicifolia*.

The stalk of the corymb may bear one to three very small foliage leaves which will be shed as flowering progresses. Trees were in flower from approximately mid January to mid

February in 1982. First external signs of flower buds were noticed in early December, 1982 and by mid November, 1983. The periods of actual flowering (opening of flowers to shedding of the petals) extended from shortly after mid February to mid March, 1983 and from about the 20th January to mid February, 1984. In the 1981/82 season, no counts were made but the crowns of most trees appeared completely white indicating a high flower density. The respective seed crop was

Figure 66. Foliage and flower corymbs of *Olearia ilicifolia*.

very good. Flowering was much less obvious in the two following seasons. Exact counts were made only for the ten trees investigated for vegetative growth. Table 14 reveals that flowering was of about the same order being possibly even slightly less in 1983/84. Seed crops, however, were almost non-existent at the end of the 1982/83 season but there were at least some filled achenes in 1983/84.

Table 14: Estimated number of corymbs per tree.

tree	PLC 1	2	3	4	5	OTR 6	7	8	9	10
1982/83	200	20	20-30	0	0	300-350	350	20	50	500
1983/84	15	60	110	5	2	70-100	300	20	180-200	150

(3) *Senecio bennetii*

Senecio bennettii flowers are born in panicles that are formed only by the terminal meristem of one year old lateral shoots (figure 67). The lateral shoot that supports the flower panicle usually sheds its foliage in the course of flowering and the complete structure dies back and aborts after achenes have dehisced. Flowering of *Senecio bennettii* thus requires two subsequent steps, the first of which is the growth of lateral branches. The number of these may vary considerably from year to year and occasionally may be lacking altogether (see section 2). The second step is that a small

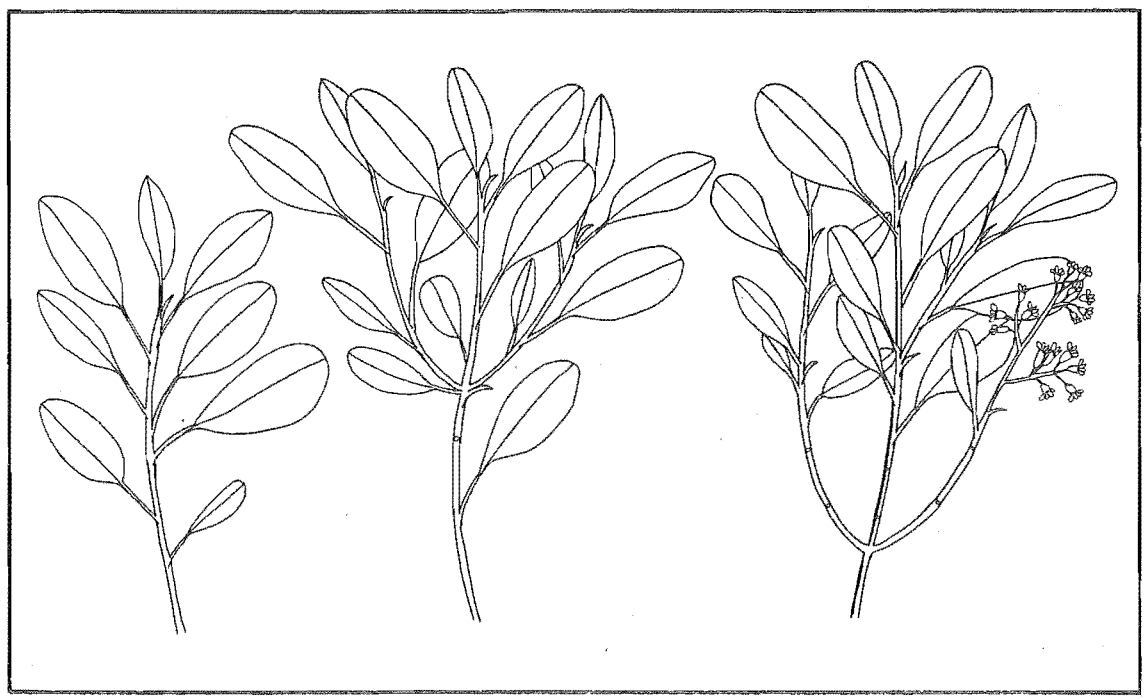

Figure 67. Morphology of the flowering shoot of *S.bennettii*.

percentage of these lateral shoots will be stimulated in some way during the first growing season (or early in the second) and switch to reproductive growth in the second summer. Two or three lateral shoots arising from the same apical shoot may act independently, some flowering, some continuing vegetative growth.

Figure 68. Flowering shoots of *Senecio bennettii*.

Senecio bennettii was in flower from late January to mid February, 1982. Flowering was virtually lacking in 1982/83 with only three individual shrubs bearing one panicle each encountered throughout the entire area. The achenes of these did not mature. Expanding buds could be identified as flower buds in early December, 1983 and flowering was widespread between the 20th January and the 10th February below 900m and about one week later at above 900m. Flowering was much more in evidence at higher altitudes from about 900m to scrubline (1000m).

Table 15: Extent of flowering of *Senecio bennettii* in 1984.

panicle / shrub	0	1	2	3	4	5	6	7	8	9	10	11 -20	21 -30	31 -40	41 -50	51 -100	101 -200	>200	S.
>900m	164	14	8	3	5	5	6	2	0	2	2	8	6	2	1	1	0	1	230
<900m	472	17	8	8	3	3	1	0	0	0	3	0	0	0	0	0	0	0	515

29% of all counted shrubs were flowering at higher altitudes compared with only 8% below 900m. The individual shrub in flower had 13.1 panicles (or at least 8.5 if the two extremes of over 50 panicles per shrub are not taken into account), but only an average of 2.8 panicles were produced at stands below 900m. The sites at lower altitudes are either on flat or slightly rolling terrain and, in one instance, on a steeper W-facing slope. The higher altitude stands are on more or less steep N to NW-facing slopes and will enjoy more sunshine and warmer temperatures. Also, competition from woody plants, both intraspecific and interspecific, is reduced at scrubline as only a limited number of species can grow successfully and woody vegetation is more sparse in general. *Senecio bennettii* is nevertheless the dominant shrub in both cases. Seed crops were good in both the 1981/82 and 1983/84 season.

(4) *Dracophyllum traversii*

Flowers are born in terminal panicles, the terminal meristem is exhausted in the process of reproductive growth and the complete shoot will usually die back some time after flowering unless sidebranches evolve from the axils of the remaining foliage leaves (figure 69). After induction to flowering which occurs at some stage during the previous growing season, flower buds are formed from all axillary buds of the still growing foliage leaves of the particular shoot.

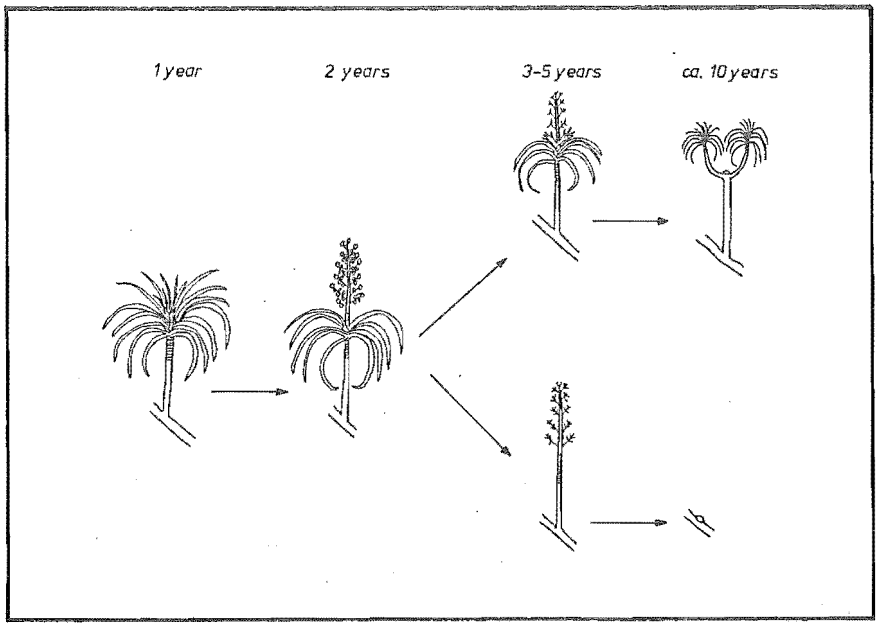

Figure 69. Development of a terminal flower panicle in *Dracophyllum traversii* and subsequent fate of the flowering shoot.

The axillary buds of older leaves that have attained their full length are not involved and probably have already aborted. While the flower buds grow in size, the leaf bases of the supporting leaves extend to several times their original breadth forming a pouch like cover around the flower buds (figure 71). This swelling of the flower buds is already externally visible by the end of the current growing season in March to April. Further growth seems to be arrested during the cold months but growth resumes and accelerates at the beginning of the following, i.e., the respective flowering season. The extension growth of the panicle axis is so fast that the already fully grown panicles were first seen in early to mid December, 1981 and 1982, without any former indications of flowering being noticed. A more careful investigation during the 1983/84 season revealed considerable swelling of some terminal leaf tufts by mid October. By mid November all younger leaves that supported flower buds were shed in a green and obviously fresh state. Each axillary

Figure 70. Terminal tuft of *Dracophyllum traversii* bearing flower buds (not visible) with an extended central axis.

Figure 71. Partly developed flower panicles of *Dracophyllum traversii* (most of the leaves have been removed).

Figure 72. Extending flower panicle of *Dracophyllum traversii*.

Figure 73. Panicle of *Dracophyllum traversii* soon after flowering.

bud subsequently forms one branch of the complete panicle; branches are forked one or two times. The individual panicle branches grow in a horizontal position and soon open their flowers. Flowering was in progress by end November to early to mid December. In the 1984/85 season flowering occurred during the second and third week of November due to the warmer winter and spring temperatures.

Flower panicle counts were made in 1982, 1983, and 1984, covering most of the investigation area (table 16). The panicles were counted using field glasses and some may have escaped detection but as the same method was employed each season counts are comparable though the actual number may be slightly higher. During the 1982/83 season flowering was clearly less in evidence, only 22% of the counted trees flowered with an average of 2.2 panicles each. In 1983/84 the percentage of flowering individuals was 43% with an average of 2.3 panicles per flowering tree. In 1984/85 flowering was both widespread and heavy, 83% of the adult individuals were in flower bearing an average of 8.8 panicles.

Table 16: Extend of flowering in *Dracophyllum traversii*.

panicle / tree	0	1	2	3	4	5	6	7	8	9	10	11 -15	16 -20	21 -25	26 -30	>30	Sum	flg.
1982/83	90	10	6	4	2	1	-	1	-	-	-	-	-	-	-	-	115	22%
1983/84	60	17	7	5	5	2	2	3	-	-	2	-	-	-	-	-	105	43%
1984/85	21	12	7	9	9	8	4	6	7	3	8	11	9	6	2	1	123	83%

If the complete adult population is considered, individual trees were bearing an average of only 0.5 panicles in 1982/83, 1.2 panicles in 1983/84, but 7.3 panicles in 1984/85. Table 17 gives exact figures for eight individual trees that

were examined since 1981/82. These counts reveal the reduced flowering incidence in 1982/83 compared with the 1981/82 and 1983/84 seasons which are comparable with regard to the extend of flowering. Flowering in 1984/85 must probably be regarded as unusual in both its extend covering almost all of the population and the high numbers of panicles of individual trees.

Table 17: Number of flower panicles of 8 sample trees.

sample tree	1	2	3	4	5	6	7	8	sum	$\bar{x}$
old panicl.	34	33	25	22	14	n.d.	23	27		
1981/82	5	2	0	13	0	9	4	6	39	4.9
1982/83	1	0	0	2	3	3	4	0	13	1.6
1983/84	11	2	1	6	5	0	7	10	42	5.25
1984/85	31	23	16	14	17	1	5	21	128	16.0

10. ESTIMATES FOR ANNUAL SEED PRODUCTION OF INDIVIDUAL TREES

Table 18 gives estimates for the average annual production of total and sound seeds for the four subject species. The estimates for *Hoheria* and *Senecio* are based on flower counts in the 1983/84 season only, however, the seed crop of this season is supposed to be representative as a mean figure as well. For *Olearia* observations for 1982/83 and 1983/84 were available but are supposed to be underestimates of the mean seed crop; the 1981/82 and 1984/85 seasons produced or most probably will produce larger crops. Flower panicles of *Dracophyllum* were counted from 1982/83 to 1984/85 and the mean number of seeds per tree will be a good estimate as the observations included two seasons of low to medium production and the 1984/85 season with a supposedly larger than average

crop.

Hoheria glabrata flowers were not individually counted but a mean number of 65 fascicles per apical shoot and 3 fascicles per lateral shoot was employed for the calculation of total flowers and seeds of a young tree, probably about 15 years old. This gave an estimate of more than 20,000 sound seeds out of a total production of 31,565. Flower numbers of adult individuals are hard to estimate as the crowns are inaccessible.

Table 18: Estimates for annual seed production.

		units* / tree	cap/fl / unit*	seeds / cap/fl	seeds / tree	sound seeds	annual seed crop
Hoheria		960	3	13.7	31,565	65.4%	20,643
Olearia	mean	121	34.2**	16.6	88,800	20.8%	14,300
	max.	500	"	"	367,000	"	59,100
Senecio	GOT	0.23	20.2**	23.6	110	39.5%	43
	SCL	3.75	"	"	1,788	"	706
	max.	200	"	"	95,344	"	37,660
Dracoph.	mean	3	2,500	335	2.5 M	3.0%	75,000
	max.	30	"	"	25 M	"	750,000

*fascicles, corymbs, panicles. **undeveloped corymbs/panicles not counted.

In corymbs of *Olearia* and panicles of *Senecio* the youngest capitula are not fully developed and remain closed. They do not produce any filled achenes, therefore, a mean number of 10 capitula per corymb (*Olearia*) and 4 capitula per panicle (*Senecio*) have already been deducted from the data given in table 18.

The mean seed crop of 14,300 filled achenes in *Olearia* is based on the observation of the ten sample trees in 1982/83 and 1983/84 when total numbers of corymbs per tree were counted or estimated. A maximum of 500 corymbs was noted in

one instance and would account for a total of 367,000 achenes 59,000 of which would be filled. This figure is supposed to be representative for the expected 1984/85 seed crop.

In *Senecio bennettii* two different populations of shrubs growing at altitudes below and above 900m, respectively, have been treated separately. In the population at lower altitude the individual shrub produced an average of only 43 filled achenes from 0.23 flower panicles as only 8% of the shrubs actually flowered in 1983/84. Above 900m 29% of the shrubs were in flower bearing 3,75 panicles each; this accounted for an average of 706 filled achenes per shrub. One individual with more than 200 panicles would have produced a total of 95,000 achenes including 37,700 sound ones.

In *Dracophyllum traversii* the number of flowers per panicle was estimated at about 2,500, giving rise to 837,500 seeds 25,000 of which would be developed. Panicle counts during the three seasons from 1982/83 to 1984/85 gave an average of 3 panicles per tree producing an estimated seed crop of 75,000. A tree bearing 30 panicles (observed in 1984/85 only) would be able to produce three quarters of a million viable seeds. It should be noted that the 1984/85 season will account for 81% of the total flower and seed production of the three observed seasons.

The comparatively low number of potentially viable achenes in *Senecio bennettii* combined with the fact that only a small percentage of the total population actually flowers and flowering may be lacking altogether in certain years,could be limiting for the reproduction of the species. During the occasional season with a heavy seed crop, like the one expected for 1984/85, all other trees and shrubs

produce by far larger crops as well and compete for the seedling habitats. At Arthur's Pass the comparatively low seed production of *Senecio bennettii* may be counterbalanced by the high number of individuals per unit area and a good regeneration of the stands may be ensured. In most other areas, however, *Senecio* is much less represented in the subalpine scrub and is usually subjected to browsing by deer. Here the relatively low reproductive ability may limit regeneration even after browsing pressure would cease.

11. SEED DISPERSAL AND REGENERATION

(1) *Hoheria glabrata*

The dry lobed fruit of *Hoheria glabrata* separates into up to 15 one-seeded cocci of 8-11mm length; the wings are only very small. The black smooth seed is about 3mm long. The one-seeded coccus is the dispersal unit, it has an average weight of 5.0±0.5mg (air dry) and is wind dispersed. The pulpy mesocarp of the coccus enables it to float in the air for a short time, the outward bent vestigial wings reduce the velocity of the fall by producing a spinning movement. This only works when the seeds are dry. The vast majority of the seeds fall within a few metres of the parent trees where the seedlings encounter strong competition from ferns, especially *Polystichum vestitum* and in places dense *Ourisia macrocarpa* clumps, but even in the absence of a herb layer seedlings are unlikely to mature because of the often dense shade from the canopy trees. Regeneration of *Hoheria glabrata* forest is, rather, by sucker shoots from old trees. Seedlings have a better chance of getting established outside the forest on bare ground like shingle fans, river banks and recent slips.

There is some pioneer growth of *Hoheria glabrata* saplings along the banks of Pegleg Creek and along the road banks of State Highway 73, especially around the parking area at the start of the upper Otira walking track and at the slopes around the former shingle pit opposite Lake Misery. Most saplings reveal their age by external indications and it was calculated that many of them must have been established from seeds of the 1974/75 flowering season. The climatic records show this as a particularly warm summer with above average temperatures from October to March which must have produced a high seed crop, increasing the chance dispersal to sites further away from the parent trees.

(2) *Olearia ilicifolia*

Olearia ilicifolia achenes are of 2mm length with a 3mm long pappus of simple bristles. The dry achenes are very light (0.3mg) and may be airborn for several minutes in light wind and dry weather. The average distance covered is supposed to be between 10-50m but occasionally, several hundred metres may be accomplished. With few exceptions, seedlings were only encountered on bare soil, both on freshly deposited material and on slip surfaces.

(3) *Senecio bennettii*

Senecio bennettii achenes are slightly larger than those of *Olearia ilicifolia*. The achene proper is 3mm long with an additional 3mm long pappus of simple hairs. The dry weight is 0.8mg. The achenes are wind dispersed, but with regard to their slightly larger size and weight, are supposed to be less efficiently dispersed than *Olearia ilicifolia* achenes. Young seedlings of *Senecio bennettii* are widespread

under forest canopy but, for the most, restricted to special "seedling habitats" like tree stumps, fallen logs and on top of boulders. Only few were seen in open scrubland and none on early successional sites.

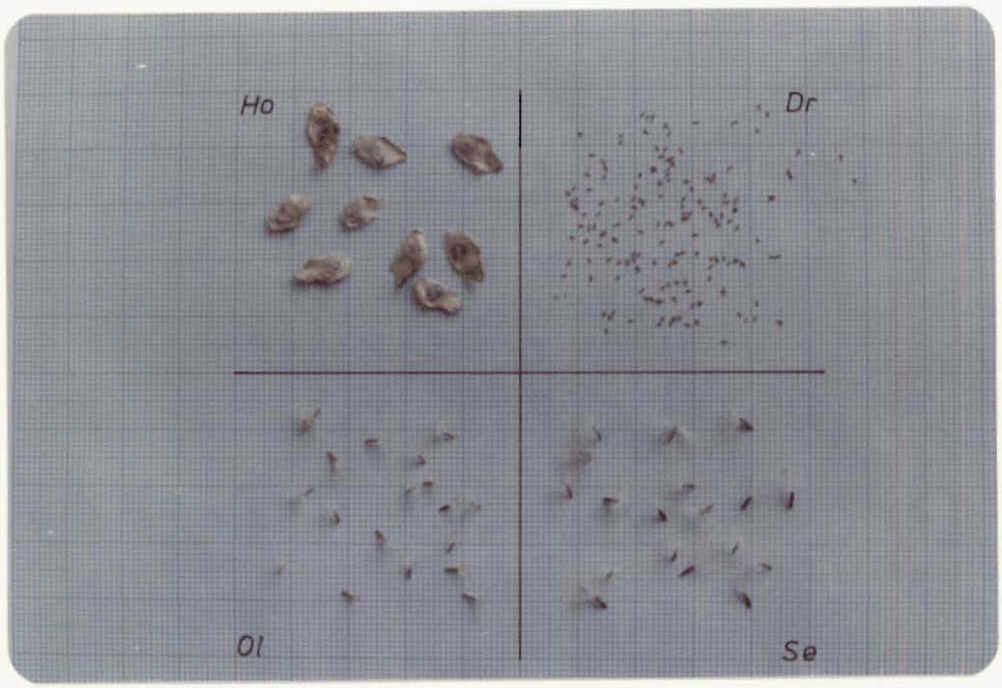

Figure 74. The seeds (dispersal units) of the four species.

(4) *Dracophyllum traversii*

The fruit of *Dracophyllum traversii* is dehiscent. Matured seeds are only slightly more than 1mm long and weigh about 0.07mg each. The light brown seed coat does not possess any special appendices facilitating dispersal but the very low weight will ensure dispersal by wind. Well growing seedlings are only seldom found beneath the forest canopy, but are more numerous in scrubland where they are mainly established on stumps, logs and boulders. Seedlings are common within up to 30-40m from the nearest parent tree but the odd seedling was also found several hundred metres away and above the limit of the scrubline. The species seems to be very

Figure 75. Typical seedling habitat on fallen log within the subalpine low forest; seedlings of *Libocedrus bidwillii*, *Phyllocladus alpinus*, *Senecio bennettii*, and *Pseudopanax simplex* are present.

Figure 76. Seedling habitat on top of a boulder with seedlings of *Dracophyllum traversii* and *Senecio bennettii*.

sensitive to waterlogged ground. Its distribution is restricted to medium to steep slopes where drainage is not impeded and trees hardly ever occupy the level terrace surfaces.

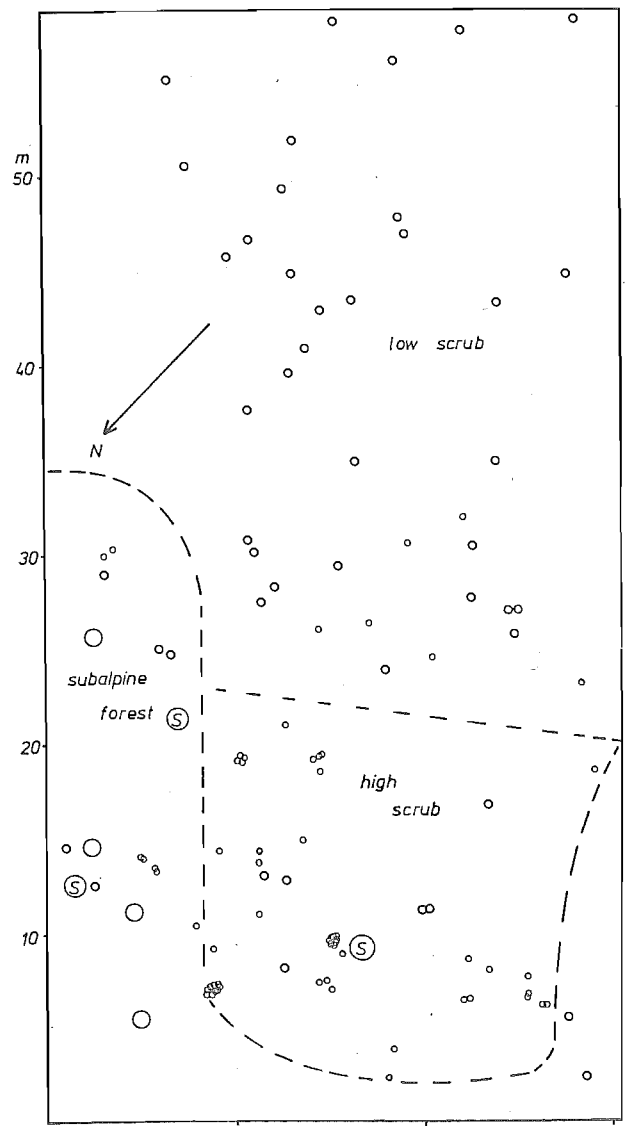

Figure 77. Spatial distribution of *Dracophyllum traversii* seedlings and saplings (larger circles) in scrubland bordering the subalpine low forest. The location of seed trees is indicated.

(5) Experimental determination of the rate of fall of seeds

In order to obtain objective figures for the dispersal ability of the seeds the rate of fall in still air was determined experimentally. Individual seeds (cocci, achenes) of each species were dropped from five metres height (indoors) and the time to reach the ground was recorded. Mean rates of fall, calculated from 20 trials for each of the species, were then expressed in metres per second (table 19).

Table 19: Mean rates of fall of seeds.

	Hoheria	*Olearia*	*Senecio*	*Dracophyllum*
rate of fall:	1.4	0.6	0.9	1.4 m/s
range	1.2-1.7	0.3-1.0	0.7-1.2	1.2-1.7 m/s

The figures clearly demonstrate the better adaptation of the composite achenes to wind dispersal. The larger variation in the composites is due to the differing seed weight and varying posiitons of the pappus hairs; lowest rates of fall are achieved with the bristles in fully vertical position. In a further outdoors experiment seeds were released at a height of five metres above ground at a wind speed of approximately 2m/s, as calculated from the readings of a cup anemometer. *Hoheria, Dracophyllum* and most of the *Senecio* seeds all fell within a distance of about 10m downwind; this equals twice the height of release. Only some *Senecio* and most *Olearia* achenes were blown further away but the actual distances could not be ascertained as the achenes were soon lost sight of, but at least 50m were covered.

The seeds of all four subject species are adapted to wind dispersal but, except for the composites, only short

distances are usually covered by the bulk of the seeds. Another means of dispersal may be downslope transport by running water, especially during heavy rain, but this form of dispersal is usually connected with deposition of the seeds at certain substrates only (shingle deposits, talus fans), which will suit *Hoheria* and *Olearia* seedlings but not the two other species.

(6) Extent of ground cover and light intensity on the forest floor

Light intensity was measured with a LI-COR lightmeter, model LI 185a. The sensor was held horizontally during the readings. Readings were taken along a 2m transect at 20cm intervals, or only minimum and maximum intensities within a specified area were noted and compared with the actual full sunlight under a cloudless sky in October, 1984.

In forests dominated by *Hoheria glabrata* the ground cover is usually made up by *Polystichum vestitum* to the exclusion of most other species (90-95%). Bare ground only occurs between the clumps of fern where runoff after heavy rainfalls clears away the litter, but eventual seedlings, too. In mixed *Hoheria* forests, i.e., stands where *Hoheria glabrata*, *Olearia ilicifolia*, and *Griselinia littoralis* make up the canopy (e.g. sample plots 12, 20, 25, 33), total ground cover is on average 50-60%, most of it still *Polystichum vestitum*, but *Blechnum capense* and *Ourisia macrocarpa* may also be important besides a number of other less prominent species. The herb and fern cover varies considerably within short distances depending mainly on the particular overhead canopy tree species. Crowns of *Griselinia littoralis* cast the most heavy shade, only 0.2-0.3% of the full sunlight (13-16µE out

Figure 78. Subalpine low forest of *Hoheria glabrata* at HGF with typical dense undergrowth of *Polystichum vestitum*.

Figure 79. Dense cover of *Blechnum capense** under subalpine scrub with a sapling of *Dracophyllum traversii*.

*This fern should rather be mentioned as *Blechnum* sp. aff. *capense* (C.J. Burrows, pers.comm.) but as the name *Blechnum capense* is still widely used it has been maintained throughout this study.

of 4,650μE) penetrate to the ground. No herbs or ferns can grow here, only occasional heavily suppressed seedlings of *Griselinia littoralis, Myrsine divaricata, Coprosma spp.* and some *Hoheria glabrata*. *Olearia ilicifolia* crowns allow much more sunlight to pass, the measured 100-700μE account for an average of 5% of the unobstructed radiation intensity. *Hoheria glabrata* trees allow still higher light levels and the ground flora is dominated by ferns. The ferns, however, reduce light intensities at the soil surface to about 0.5% but the cover is never completely closed. Numerous sunflecks in the forest, especially early in the season when *Hoheria glabrata* is still bare and evergreens have a minimum amount of foliage, allow an almost unobstructed light intensity to reach the ground (80-90%). Small sunflecks arising from gaps in the foliage of individual trees were found to have light intensities in the order of 300-900μE which accounts for 5-20% of the full sunlight. Total ground cover in stands of these mixed forests was approximately 40%, most of it *Blechnum capense* with *Polystichum vestitum* being less important. Whereas *Polystichum vestitum* grows as single tufts of fern, though usually gregarious, *Blechnum capense* has a creeping rhizome and forms dense patches of fern which are continuously extending; the soil beneath becomes covered with its litter. This prevents establishment of seedlings on the ground. They can only be found on tree stumps and logs where they escape competition, especially for sunlight.

Blechnum capense ground cover is still more pronounced in the forest types dominated by *Dracophyllum traversii* and *Phyllocladus alpinus*, where it accounts for most of the 60-70% total ground cover. Successful seedlings of trees and

shrubs are restricted to the above mentioned microhabitats. The same conditions apply for the stands of successional scrub dominated by *Senecio bennettii*. The tree saplings that are now established here must have come in immediately after the fire before the ground was covered with *Blechnum capense*.

12. SEEDLING SURVIVAL IN SAMPLE QUADRATS

The 1981/82 season produced an average to good seed crop, therefore, density and survival of seedlings could be monitored for the following two years. Three 50 x 50cm frames had been laid out at both *Hoheria - Olearia* stands at OTR and PLC, another two on a recent shingle deposit near PLC. Two frames each were situated in subalpine low forest with *Phyllocladus alpinus* and *Dracophyllum traversii* at SAF and HTS.

(1) *Hoheria glabrata* seedlings

Hoheria glabrata seeds were present on the ground in great quantities and most seeds germinated in late September, 1982. Germination (radicle emergence) was about one week earlier (prior to the 22nd September) at the shingle deposit (less canopy, N-facing slope) than in other locations. By the end of October most seedlings had their cotyledons fully unfolded but only one or two primary leaves were produced until the end of the season. All seedlings had their cotyledons shed at the beginning of June. Only during the first year was it possible to distiguish the new seedlings from older ones that were probably one to three years old. Later both age classes had to be lumped together because further growth was too slow to allow a clear cut categorization.

Table 20: Seedling survival in *Hoheria glabrata*.

	forest floor	shingle deposit	
December 1982	280+(48)*	900+(425)*	seedlings/m^2
April 1983	216	340	seedlings/m^2
December 1983	184	276	seedlings/m^2
April 1984	116	200	seedlings/m^2

*seedlings that were 1 year and older by December, 1982

Seedling counts at the beginning of December, 1982 showed mean densities of 280 seedlings/m^2 (average of 6 sample quadrats of 0.25m^2 dimension) on the forest floor and 900/m^2 on the fresh shingle deposit. An additional 48 older seedlings per squaremetre were also present at the former sites and 425/m^2 of these category at the shingle deposit. Seedling mortality was high during the first growing season. By the end of April, 1983 an average of 216 (340)/m^2 remained. Most of these seedlings survived the winter (the subsequent December count was 184 (276)/m^2) and by the end of April, 1984, there were only 116 (200)/m^2 left. Not one of these revealed any considerable growth and it is supposed that all of them will die within two or three years. Seedlings and saplings that showed remarkable growth during the first few years were the exception, only very few were encountered throughout the investigation area. There were no *Hoheria glabrata* seedlings in the sample quadrats in the subalpine low forest dominated by *Dracophyllum traversii*, though scattered *Hoheria glabrata* individuals that could serve as seed sources occur nearby. Only one seed was seen germinating within the quadrats but its radicle failed to become established in the soil.

(2) *Olearia ilicifolia* seedlings

Though *Olearia ilicifolia* produced ample seed early in 1982 no seedlings could be located during the subsequent season. It was only in December, 1983, after the less pronounced seed crop of 1982/83, that four seedlings were found in one of the quadrats on the talus fan. Both quadrats had received an additional influx of gravel and sand (which buried and killed many *Hoheria* and *Griselinia* seedlings) after heavy rain during late December, 1982. A few more new seedlings were seen nearby on bare ground at the source of a slip. Older *Olearia ilicifolia* seedlings, having made good progress, were found only in one location. With regard to the ready germination (see section 1, chapter VII) it seems surprising that only so few *Olearia* seedlings could be located. However, its achenes are more easily dispersed by wind and most will settle where conditions are unfavourable for growth and soon die because of the limited seed reserves. *Hoheria* seeds, on the other hand, are not particularly well adapted to wind dispersal and will be found in higher densities around the parent trees. Larger nutrient reserves of the seeds allow for initial growth independent from the conditions on the forest floor. Nevertheless, after two or three years, they ultimately fail to become established. Different light requirements for germination will also be responsible for the discrepancies in seedling densities of *Hoheria* and *Olearia* (see section 1, chapter VII).

(3) *Senecio bennettii* seedlings

Senecio bennettii seedlings were found in low densities of one, two or three per quadrat in both types of sub-

alpine low forest. Only two of the quadrats showed exceptional numbers of 7 and 20, respectively. The seedlings form only a rosette of leaves without noticeable shoot extension during the first year and later on, only a few, usually growing at sunflecks (on logs), will make considerable progress and become established. No seedlings were found growing on recently disturbed sites.

(4) *Dracophyllum traversii* seedlings

Dracophyllum traversii produced seed during all of the observed seasons but not one first year seedling was ever discovered. There are, however, some older seedlings (probably more than five years old) throughout the subalpine low forest at SAF, often growing together in small groups. Some saplings encountered here show only poor growth under the forest canopy and will probably die sooner or later. Seedling and sapling growth was more promising in the open *Senecio bennettii* scrubland to the south of the subalpine low forest stand, where a secondary succession after the 1878 (or 1890) fire is still in progress. Almost all of these older seedlings are established on stumps and logs, remnants of the former burnt forest.

13. ANIMAL INFLUENCES

(1) Pollination

Pollination is supposed to be entomophilous in all four species under consideration. My records for insects associated with *Hoheria glabrata* flowers include thrips (Thysanoptera), weevils and other small beetles. Though the mentioned insects may contribute to pollination they are

mainly concerned with feeding on the pollen. Recently, S.A. Norton stressed the importance of thrips pollination in New Zealand forest trees and identified *Thrips obscuratus* on a variety of trees including *Hoheria sexstylosa* (Norton, 1984). The sweet-scented showy white flowers of *Hoheria glabrata* are presumed to attract a number of nocturnal moth species (C.J. Burrows, pers.comm.). Heine (1937) mentions numerous diptera and lepidoptera for the related *Hoheria sexstylosa* and *Hoheria populnea*.

Visitors on flowers of both *Olearia ilicifolia* and *Senecio bennettii* were small beetles, mostly of the family Dascillidae (presumably *Cyphon spp.*) and weevils, family Curculionidae. Heine (1937) reports the same family of beetles on flowers of *Olearia lacunosa* and *Senecio elaeagnifolius* as well as numerous flies and native bees. Wardle (Wardle et al, 1971, citing J.S.Dugdale) mentions that weevils were feeding on the pollen of *Olearia colensoi* and may contribute to the transfer of some pollen between individual flowers.

Small diptera were observed on the flowers of *Dracophyllum traversii*, unidentified small beetles including weevils were also among the visitors. Heine (1937) also mentions beetles (Melysidae, Curculionidae) for two smaller *Dracophyllum* species.

(2) Predators

Caterpillars of at least two moth species were found feeding on the foliage of *Hoheria glabrata* during April/May, 1982 but were less frequent the following years. Hudson (1928) mentions the larva of the Notodont moth *Epiphryne (Venusia) undosata* as a foliage feeder on *Hoheria glabrata*. On two occasions young *Hoheria* trees were seen infested with

galls presumed to be caused by parasitic Eriophyid mites. The larva of a small moth, believed to be *Simaethis combinatana*, family Glyphipterygidae, feeds on the seeds of *Hoheria*. Morrison (1933) noticed this moth larva as a seed predator on *Hoheria lyallii* trees at Lincoln (cultivated individuals) and at Cass. His description of the larva and its feeding pattern fits that of the species encountered on *Hoheria glabrata* at Arthur's Pass. Morrison also notes that the larva overwinters in dead wood of *Hoheria*. Later in the season, *Hoheria* leaves show brown mottles caused by a rust fungus.

At least two species of caterpillars feed on *Olearia ilicifolia* foliage. One consumes the expanding young, not yet sclerotinized leaves during October/November, another feeds on adult foliage later in the season. One of the latter category was identified (after hatching) as the Geometrid moth *Selidosema rudiata*, family Notodontidae. Another unidentified moth larva predates the young leaves that expand later in the season by webbing the two uppermost leaves of the shoot together and then feeds on the epidermal tissues between them. Tuthill (1952) collected *Trioza crinita* and *Trioza doryphora*, family Psyllidae (plant lice) from the foliage of *Olearia ilicifolia* which are reared in pseudogalls formed by the curling edges of young leaves. These pseudogalls are common on *Olearia ilicifolia* trees at Pegleg Flat.

Shoot apex destroyers were also noted but could not be identified. An unidentified larva, probably the same as in *Senecio bennettii*, destroys the achenes; Curculionidae have been reported to do this in *Olearia colensoi* (Wardle et al, 1971).

Foliage of *Senecio bennettii* is only seldom fed on by

insects. An unidentified larva, possibly of a Chrysomelid beetle, as recorded for *Olearia colensoi* by Spain (cited in Wardle et al, 1971), occasionally destroys the shoot apex and tunnels the upper part of the shoot. Probably the same species that predates *Olearia ilicifolia* achenes was also frequently found in *Senecio bennettii* achenes. Occasionally, a profusion of minute lateral shoots is found on several years old branches (witches broom) which is thought to be caused by parasitic Eriopyid mites.

Black sooty mould on *Dracophyllum traversii* is supposed to develop on the excretions of scale insects. Green (1929) identified the scale insect *Coelostomidia montana*, family Coccidae,on *Dracophyllum traversii*. The white fluffy exudations covering the eggs can always be found under the old leaf scars and bark. This exudations are typical of the genus *Coelostomidia* (Tillyard, 1926). The foliage of *Dracophyllum traversii* is usually not predated; observed malformations of leaves may have resulted from mechanical damage. Occasionally, holes in the leaves are caused by an unidentified shoot apex destroyer that bores through the leaves into the apex. The apex usually dies but if growth proceeds, the holes made into the leaves remain visible. Another larva predates the central stem of the flower panicles and sometimes completely hollows it. On a few occasions it was observed that the seeds of *Dracophyllum traversii* were predated by a very small unidentified larva.

(3) Vertebrates

Keas (*Nestor notabilis*) were seen on several occasions during the winter feeding on young foliage and the shoot apex of *Dracophyllum traversii*. In cases where the shoot apex

survives predation, the damage is later recognizable by the blunt and torn tips of all leaves that arose from the apex at the time of predation.

Figure 80. Severe browsing damage by possum on *S. bennettii*.

During the winter of 1984, two *Senecio bennettii* shrubs were found heavily browsed by possum (*Trichosurus vulpecula*). It seemed that the animal returned repeatedly to the same shrub for feeding until virtually all shoots were defoliated, except for the old leaves (predating the 1983/84 season) which were left untouched. It is supposed that these must be of different taste and/or of lower nutritional value.

14. ESTIMATES FOR ABOVEGROUND BIOMASS AND ANNUAL PRODUCTIVITY

Tables 21 to 24 give calculations and estimates for annual productivity and aboveground biomass for individual trees or shrubs of *Olearia*, *Senecio* and *Dracophyllum*. The data collection for *Hoheria* was not sufficient to allow simi-

lar calculations for this species. Sampling was restricted to foliage, shoots, and small samples of wood and bark. Estimates for stemwood and stembark dry weight were calculated on the basis of basal diameter and average height of the sample trees. Branchwood was roughly estimated as 50% of the stemwood weight, and branchbark as 100% of the stembark weight. These factors were indicated by Lieth and Whittaker (1975, pp. 62,64,78). To calculate total bark biomass an average thickness of ten annual layers was assumed to be retained by the trees. Additional weights of petals, pollen and bud scales were not estimated but are thought to be negligible. Loss by predation is only of any importance in *O. ilicifolia*.

Table 21: Mean figures for annual production of leaves, litter, shoots, flowers, and seeds of the three evergreen species.

	season	n	ø(cm)	hght. (cm)	no. sht.	fol. (m^2)	fol. (g)	litt* (g)	sht. (g)	flow. (g)	seeds snd. (g)	seeds emp. (g)	seeds tot. (g)
SCL *Se.*	81/82					3.4	698	- -	72	- - - - - -	n.d.	- - -	
	82/83					3.5	702	616	89	- - - - - -	nil	- - -	
	83/84					3.6	731	651	94	2.3	0.6	0.3	3.2
	mean	10	8.1	117	407	3.5	711	634	85	2.3	0.6	0.3	3.2
GOT *Se.*	81/82					2.7	546	- -	-	- - - - - -	n.d.	- - -	
	82/83					2.4	487	469	34	- - - - - -	nil	- - -	
	83/84					3.2	635	484	61	0.14	0.04	0.02	0.2
	mean	10	10.6	158	348	2.7	556	477	48	0.14	0.04	0.02	0.2
PLC *Ol.*	81/82					13.7	(kg) 3.2	(kg) - -	427	- - - - - -	n.d.	- - -	
	82/83					17.1	4.0	3.0	501	6.6	1.7	3.1	11.3
	83/84					8.5	2.0	2.0	256	5.2	1.3	2.5	9.1
	mean	5	28.0	485	2136	13.1	3.1	2.5	395	5.9	1.5	2.8	10.2
OTR *Ol.*	81/82					13.8	3.2	- -	395	- - - - - -	n.d.	- - -	
	82/83					19.5	4.6	3.1	465	32.9	7.9	14.3	48.1
	83/84					10.2	2.4	1.8	233	19.5	5.0	8.5	33.0
	mean	5	n.d.	n.d.	2842	14.5	3.4	2.5	347	26.2	6.5	11.4	44.1
HTS *Dr.*	83/84	3	34.2	567	222	14.5	3.9	4.1	135	225.0	5.5	18.3	249

*litter production for the July - June period

Table 22: Estimates for annual production and standing biomass of wood and bark.

	stemwood		branchwood		stembark		branchbark	
	prod.	biom.	prod.	biom.	prod.	biom.	prod.	biom.
Se. SCL	93g	1.1kg	47g	0.5kg	7g	73g	7g	73g
Se. GOT	163g	2.4kg	82g	1.2kg	13g	128g	13g	128g
Ol. PLC	1840g	59.7kg	920g	29.9kg	322g	3.2kg	322g	3.2kg
Dr. HTS	865g	112.9kg	433g	56.5kg	153g	1.5kg	153g	1.5kg

Table 23: Estimates for mean annual dry matter production.

	wood	bark	sht.	fol.	rep.	tot.	litt.
Se. SCL	140	15	85	710	3	954	634 g
Se. GOT	245	26	48	556	0.2	874	477 g
Ol. PLC	2800	644	395	3100	10.2	6900	2500 g
Dr. HTS	1300	306 +65*	135	3900	249	6000	4100 g

*leaf scars

Table 24: Estimates for aboveground biomass (dry weight).

	wood	bark	fol.	total
Se. SCL	1.6	0.15	0.93	2.7 kg
Se. GOT	3.7	0.26	0.75	4.7 kg
Ol. PLC	89.6	6.40	4.00	100.3 kg
Dr. HTS	169.4	3.00 +0.65*	14.50	187.6 kg

*leaf scars

Annual dry matter production of shoots and foliage in *Olearia ilicifolia* reflects the annual pattern of change in leaf area per shoot and shoot length. In 1983/84 only about 50% of the 1982/83 dry weights of foliage and shoots were produced due to the decrease in shoot length, leaf area per shoot and number of lateral branches per shoot. Litterfall in terms of dry weight per tree in 1983/84 was only 60-66%

compared with the previous season, because more old leaves were retained. Wood and bark production was only calculated for the trees at PLC, the OTR individuals differ very much in dimensions and some had partly decayed trunks and branches rendering estimates unreliable.

While both stands of *Senecio bennettii* showed a decline in leaf area per apical shoot and shoot length from 1981/82 to 1983/84, there was a slight increase in terms of total dry matter production during the same period. This is due to the increased production of lateral branches (see section 2). Flowering in 1984/85 will probably contribute significantly to annual dry matter production.

Data for vegetative growth of *Dracophyllum traversii* were available for the 1983/84 season only.

Dracophyllum and *Olearia* are of comparable dimensions, annual production of new foliage is in the same order of magnitude but production of wood and bark is considerably less in *Dracophyllum* due to the lower growth rates of this species. Total aboveground biomass, especially in terms of wood and foliage, however, are higher in *Dracophyllum* due to the advanced age of the specimens (300-400 years) and the fact that foliage of about five seasons is retained on the shoot.

With regard to investment in reproduction, a flower panicle of *Dracophyllum traversii* weighs about 75g plus 8g of seeds which makes up an average of 250g of dry matter that has to be allocated to reproduction if a mean number of three panicles per tree is assumed. An additional 50g of dry matter is accounted for by the accelerated loss of all the axillant leaves of a flowering panicle, and finally, altogether about 5% of the total annual dry matter production is spent

on reproduction. Should the supporting branch abort later on, as often happens, the loss will be greater still.

15. FLORISTIC ANALYSIS OF THE FOREST AND SCRUB VEGETATION

Table 25 gives a list of 71 vascular plants that were encountered in the 35 sample quadrats. Epiphytes, like some ferns, mosses, liverworts, and lichens have not been included in the list; they are usually confined to trees and rocks. Epiphytic species of the fern genera *Hymenophyllum* and *Grammitis* occur abundantly throughout most of the investigation area and only become restricted to sheltered sites at higher altitudes and more open vegetation. *Asplenium flaccidum* and *Lycopodium varium* were also occasionally noted but these species are restricted to the more mature types of subalpine low forest. Most of the mosses, liverworts and lichens occupy epiphytic habitats as terrestrial sites and only the large moss *Dendroligotrichum dendroides* always occurs on the forest floor where it forms small clumps. Grasses and sedges were only included in the records where they were considered part of the ground flora, occasional specimens growing on top of boulders were neglected.

Two of the 71 listed species - *Senecio bennettii* and *Blechnum capense* - were found in all 35 sample plots. Five other species (*Pseudopanax colensoi*, *Coprosma pseudocuneata*, *Astelia nervosa*, *Phormium cookianum* and *Polystichum vestitum*) were encountered in at least 30 quadrats.

(1) Cluster analysis

Presence and absence of individual species from the sample plots as shown in table 25, was used for the calcula-

Table 25: List of species

	sample plot:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
conifers	*Libocedrus bidwillii*									+	+								+			+	+	+	+		+									
	Podocarpus hallii		+	+	+		+		+	+	+	+				+	+	+	+	+		+	+	+	+	+	+		+							
	Podocarpus nivalis	+			+	+	+	+																					+	+	+	+				
	Dacrydium biforme																					+														
	Phyllocladus alpinus	+	+	+	+	+	+	+	+	+	+		+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+
shrubs and trees	*Hymenanthera alpina*								+	+										+																
	Pittosporum divaricatum								+	+	+								+	+					+											
	Aristotelia fruticosa		+		+	+	+	+	+			+						+	+	+														+	+
	Hoheria glabrata	+	+		+	+	+	+	+	+		+	+	+		+	+	+	+	+	+	+	+	+		+	+	+	+						+	+
	Pseudopanax simplex								+	+	+	+											+	+	+	+		+			+					
	Pseudopanax colensoi	+	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
	Pseudopanax lineare								+	+	+											+	+	+	+		+									
	Griselinia littoralis	+	+	+		+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+		+	+
	Gaultheria antipoda																														+					
	Gaultheria depressa																											+	+			+				
	Gaultheria crassa																												+		+	+	+			
	Cyathodes juniperina																												+							
	Archeria traversii						+		+	+	+	+					+			+		+	+	+	+		+			+	+	+				
	Dracophyllum uniflorum																											+				+	+			
	Dracophyllum longifolium	+							+	+	+		+			+			+	+			+	+	+	+	+	+		+	+	+	+	+		+	+
	Dracophyllum traversii		+	+			+	+	+	+	+	+					+	+	+	+	+		+	+	+	+		+		+	+	+	+			+
	Myrsine divaricata	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+						+	+
	Coprosma rugosa	+	+		+	+		+												+	+					+		+	+	+	+	+	+			
	Coprosma depressa			+		+	+	+		+	+	+	+	+	+	+	+		+	+	+	+	+	+	+				+							
	Coprosma pseudocuneata		+	+	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+		+
	Coprosma ciliata		+		+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+		+												+
	Coprosma parviflora	+	+	+	+		+	+	+	+		+		+	+					+		+	+	+	+		+	+	+	+	+	+	+	+	+	
	Coprosma colensoi	+			+	+		+	+	+	+	+	+		+				+	+	+	+	+	+	+		+			+			+			
	Coprosma foetidissima	+								+									+	+							+									
	Coprosma serrulata	+		+		+							+					+	+	+				+		+			+		+	+	+	+		+	
	Olearia colensoi																	+																			
angiosperm	*Olearia nummularifolia*	+				+													+	+														+		+	
	Olearia avicenniaefolia	+																	+	+						+								+			
	Olearia arborescens	+																		+									+	+	+	+			+	
	Olearia "macrodonta"								+	+												+			+			+				+					
	Olearia ilicifolia	+	+		+	+	+	+			+	+	+	+	+				+	+	+	+				+		+	+	+		+	+	+	+	+	
	Senecio bennettii	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Senecio bidwillii																																			+	
	Hebe canterburiensis					+					+						+							+			+							+			
	Hebe salicifolia					+		+	+			+		+	+				+		+	+				+		+						+			
	Hebe subalpina	+	+		+	+	+	+	+		+							+	+	+	+		+	+				+	+	+	+	+	+	+		+	
vines	*Clematis australis*	+																	+		+																
	Rubus schmidelioides								+	+										+	+	+															
	Parsonsia capsularis								+											+																	
herbs	*Ranunculus lyallii*		+			+		+										+	+		+													+		+	
	Ranunculus hirtus					+								+	+	+					+														+			
	Cardamine debilis		+		+	+								+	+	+			+		+	+		+	+												
	Viola filicaulis				+																+																
monocotyledonous dicotyledonous	*Acaena spec.*																																			
	Geum parviflorum																																			
	Aciphylla horrida																																	+		+
	Celmisia spectabilis																															+				
	Celmisia coriacea																										+	+	+	+	+	+	+			+
	Celmisia armstrongii																													+						
	Ourisia macrocarpa		+		+	+	+	+		+	+		+			+	+	+	+	+	+												+			
	Astelia nervosa	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Phormium cookianum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Corybas spec.						+						+	+				+																			
	Pterostylis australis						+						+	+	+				+	+	+		+														
	Unicinia spec.					+							+																								
	Chionochloa flavescens							+						+	+		+											+	+	+	+	+	+	+		+	
	Gramineae					+			+		+																								+			
pteridophytes	*Lycopodium scariosum*																										+	+	+	+	+	+	+				
	Lycopodium fastigiatum																										+	+	+	+	+	+	+		+		
	Gleichenia cunninghamii																			+																	
	Cyathea colensoi			+			+		+		+	+				+						+	+	+	+		+			+						
	Phymatosorus diversifolius								+				+																								
	Hypolepis millefolium																									+								+		
	Blechnum capense	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Polystichum vestitum	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+					+	+	+
	*Mycelis muralis**	+	+		+	+		+			+	+	+	+			+	+	+	+						+								+		

*adventive species

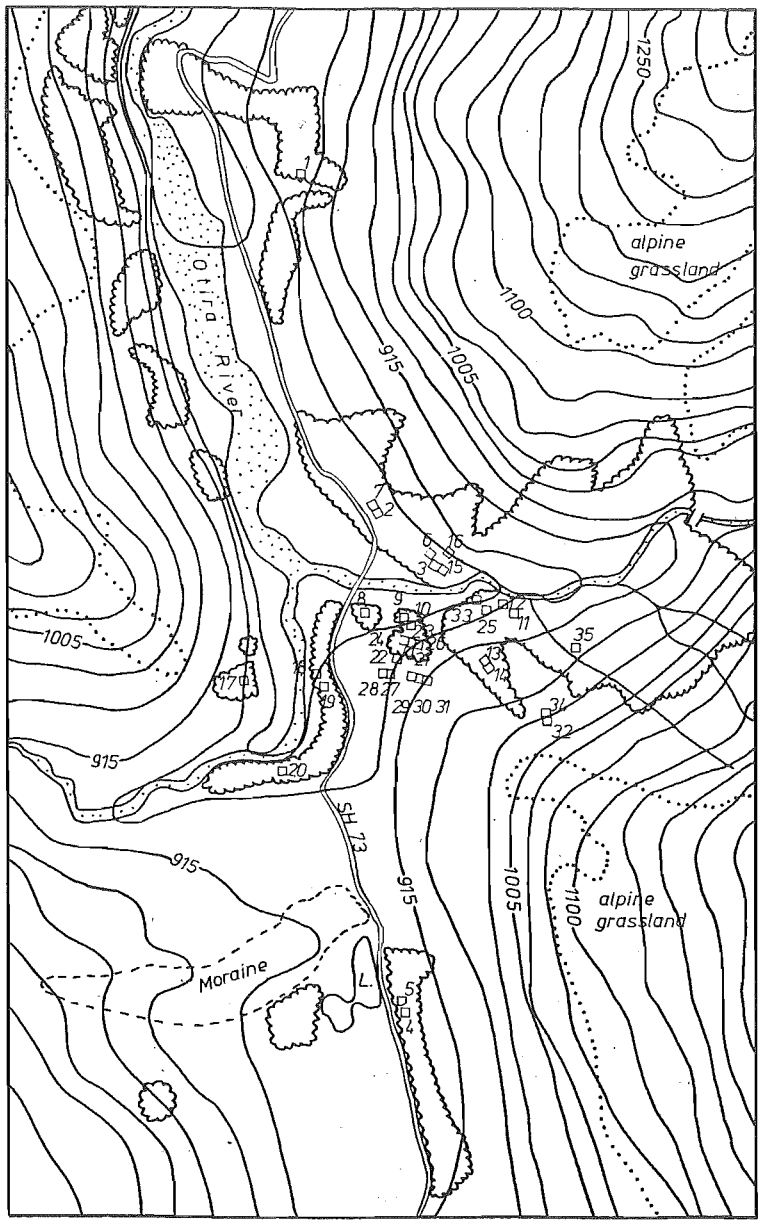

Figure 81. Location of the 35 sample quadrats.

tion of the community coefficient after Sørensen ($CC=\frac{2C}{A+B} \times 100$) and a subsequent cluster analysis. Figure 82 shows the dendrogram of this analysis. The average linkage sorting method was employed and all calculations were performed by hand using a pocket calculator.

The dendrogram allows a differentiation into six clusters or groups of stands and three single outliers, the stands 1, 11, and 35. The first cluster (group III) comprises eight stands that are all situated at the N to W-facing slopes of Phipps Peak and the high terrace slope S of Pegleg Creek.

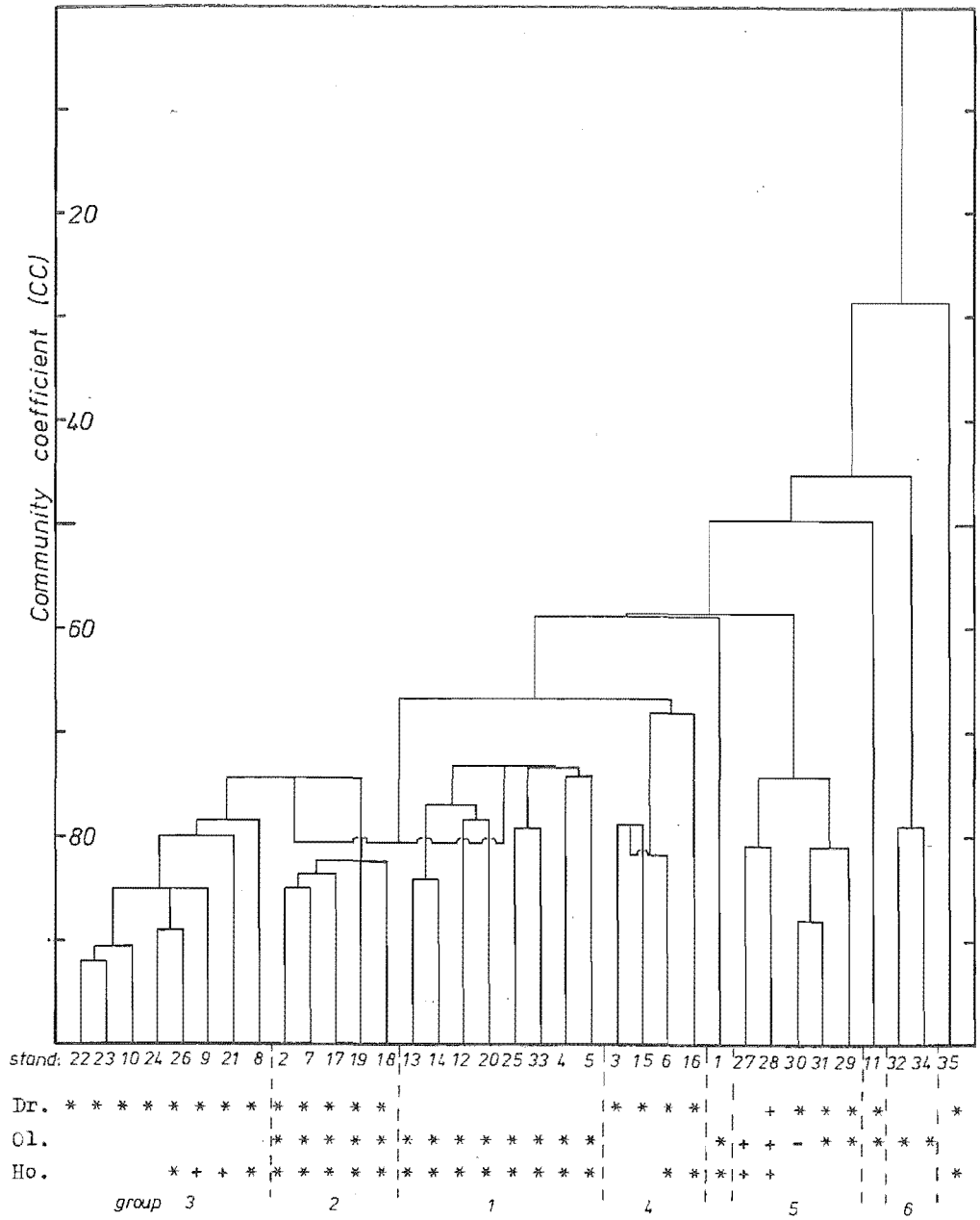

Figure 82. Dendrogram of a cluster analysis of the 35 sample plots. The presence of *Hoheria*, *Olearia* and *Dracophyllum* is indicated by an asterisk. +, few saplings present but not regarded established; -, species not present in the particular quadrat but typical in the type of vegetation.

These sites support stands of dense subalpine low forest that is characterized by the presence of *Libocedrus bidwillii*, *Podocarpus hallii*, *Phyllocladus alpinus*, *Pseudopanax simplex*, *Griselinia littoralis*, and *Dracophyllum traversii* as the main

canopy species. The ground cover consists mainly of *Blechnum capense* with occasional *Cyathea colensoi*. The four stands 3, 6, 15, and 16 that occupy the S to SW-facing slopes N of Pegleg Creek make up another cluster (group IV). These stands differ from the former by the absence of a number of species that are considered to prefer warmer sites (*Libocedrus bidwillii, Podocarpus hallii, Pseudopanax simplex, Coprosma foetidissima*). Only *Phyllocladus alpinus, Griselinia littoralis* and *Dracophyllum traversii* remain as the main canopy species. The ground flora is again dominated by *Blechnum capense*, the fern *Cyathea colensoi* occurs as well and seems to be restricted to these two types of forest. The dendrogram does not reveal the apparent relationship of the two associations; the latter may be considered a depauperate subassociation due to unfavourable aspect of the site. The relationship is far better represented by the polar ordination diagram (see following subsection).

Another cluster is formed by the stands 2,7,17,18,19, which occupy a transitional status between tall scrub and low forest and contain the highest number of species. The stands are usually associated with old talus fans and therefore species with a demand for higher soil fertility are common (*Hoheria glabrata, Olearia ilicifolia, Pseudopanax colensoi, Griselinia littoralis*), but a few, usually younger individuals of the subalpine low forest like *Libocedrus bidwillii, Phyllocladus alpinus* and *Dracophyllum traversii* also make their appearance. Remnants of early successional phases like *Olearia nummularifolia, O.arborescens, O.avicenniaefolia* and *Hebe salicifolia* may also still be present. The ground flora is dominated by a mosaic of *Blechnum capense* and *Poly-*

stichum vestitum but also contains other species like *Ourisia macrocarpa, Ranunculus lyallii, Pterostylis spec.*, etc.

A further recognizable cluster of stands (group I) with similar vegetation consists of the four pairs of stands 13,14; 12,20; 25,33; and 4,5. These stands occupy the most fertile sites (corresponding to the soil pits 1,2,3); the forest is dominated by *Hoheria glabrata* and *Olearia ilicifolia* and the ground flora consists sometimes almost exclusively of *Polystichum vestitum* with some *Blechnum capense* and occasional patches of *Ourisia macrocarpa*.

Group V contains the sample plots 27-31 that are situated in a successional scrub dominated by *Senecio bennettii* in an area burnt by the 1878 and/or 1890 fire. The original vegetation was a subalpine low forest similar to that of the adjacent stands of group III. The scrub will probably revert to subalpine forest within the next 100-200 years or so; saplings of *Dracophyllum traversii* are a common feature and occasional saplings of *Libocedrus bidwillii, Phyllocladus alpinus* and *Pseudopanax simplex* were also noticed. The ground flora of lycopods, Celmisias and *Chionochloa flavescens* accounts for most of the floristic differences compared to the subalpine low forest proper.

The two scrubline stands (group VI) are only linked to the other stands at a CC-value of 45 because alpine herb species make up most of the vegetation cover.

The stands 1 and 11 fit only poorly into any of the tentative groups of related stands; sample plot 1 may be associated with group I or II, whereas stand 11 could be attached to group III, as indicated by the polar ordination diagram. Stand 35 is related to group III or IV but posses-

ses a much reduced number of species as a result of the near absence of a shrub and herb layer.

(2) Polar ordination

The calculated CC-values (Sørensen, presence only) were transformed into ID-values (index of difference, ID = 100-CC), and the individual stands were spread out two-dimensionally in a polar ordination diagram as described by Barber et al, 1980). Figure 83 shows the resulting diagram. Putative associations that were recognized with the aid of the cluster analysis have been enclosed by broken lines. The diagram reveals that most of the stands are spread out vertically (along axis 2) only, and only the stands with scrubland vegetation have been spread out along axis 1. It was concluded

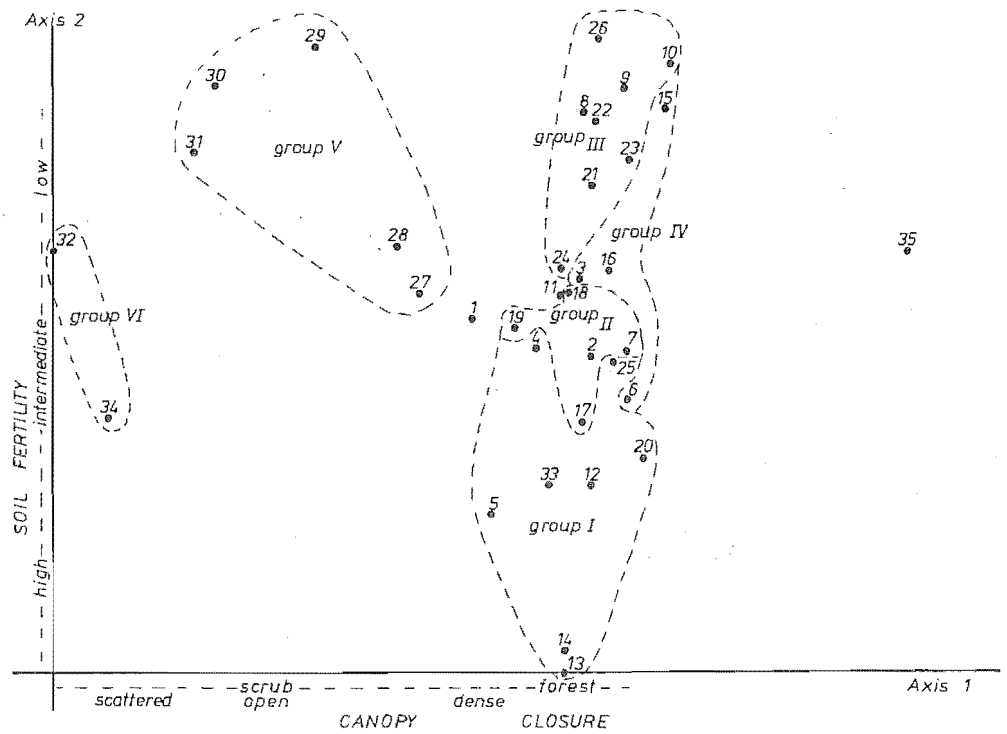

Figure 83. Polar ordination diagram with presumed environmental gradients (canopy closure, soil fertility) indicated.

that axis 1 relates well to the increasing extent of canopy closure, with stands 32 and 34 representing scattered scrub (scrubline), stands 27-31 open scrub (successional scrub), and 1 and 19 dense scrub. All remaining sample plots support subalpine low forest. Stand 35 (used as a reference stand for the construction of axis 1) supports subalpine low forest dominated by *Dracophyllum traversii* with a very dense canopy that almost excludes any undergrowth. Axis 2 can be best interpreted as a soil fertility gradient. The results of the soil nutrient analyses support this view, as well as the general floristic composition of the particular stands.

(3) Distribution of the subject species in the putative associations and along environmental gradients

The presumed soil fertility gradient along axis 2 can be further demonstrated by using *Hoheria glabrata* as an "indicator" species for high soil fertility. *Hoheria glabrata*

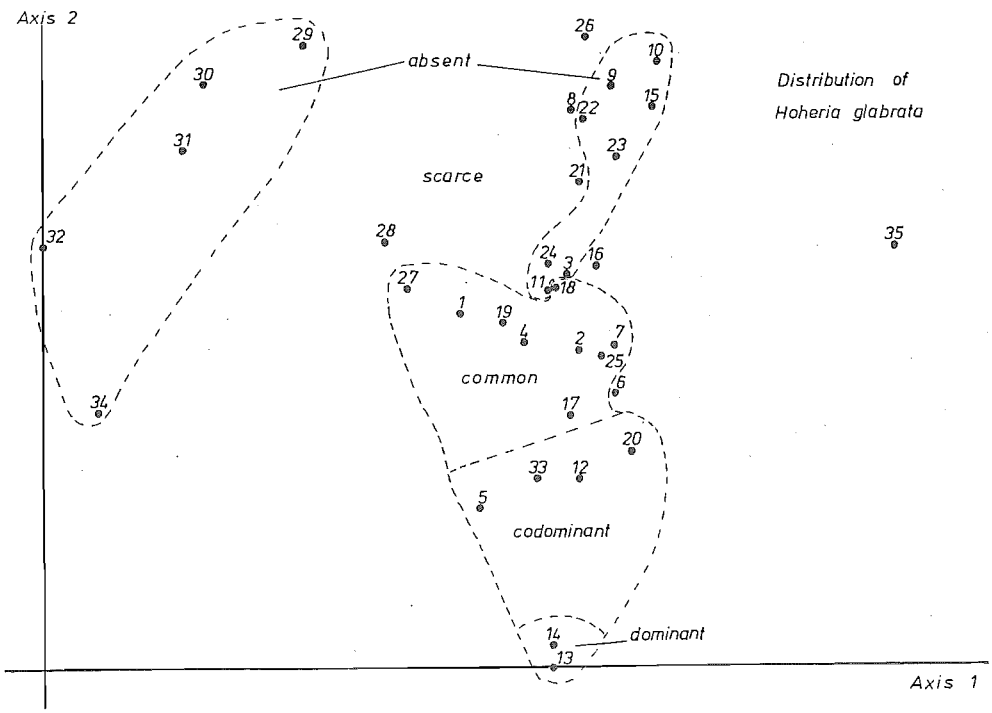

Figure 84. Relative abundance of *Hoheria glabrata*.

is the dominant to almost exclusive tree in the stands 13 and 14 (HGF) and the analyses of the respective soil samples revealed the highest nutrient concentrations. Soil fertility was lower in the samples from soil pits 1 (OTR) and 2 (PLC), corresponding to the stands with *Hoheria glabrata/ Olearia ilicifolia* co-dominance. *Hoheria* is still common, though of minor importance, in the stands with intermediate status but scarce to absent in associations on leached and less fertile soils. Absence of *Hoheria glabrata* from the stands 29-32 and 34 is believed to be primarily due to low soil fertility as well, and not to increasing altitude as might be supposed. At disturbed sites with good drainage and in somewhat sheltered positions *Hoheria* may form groves of low forest at considerable altitudes and constitute the treeline.

Olearia ilicifolia also prefers sites with high soil fertility where it grows as a small tree of 4-8m height (lower half of figure 85). As a member of scrub vegetation *Olearia ilicifolia* is adapted to develop the growth habit of a shrub and can even ascend above treeline. In these vegetation types it usually occurs together with *Olearia arborescens*, which is confined to scrub and forest margins, and *Olearia "macrodonta"*, which is probably a hybrid form between the two latter species (left part of figure 85). *Olearia ilicifolia* is absent from the subalpine low forest associations dominated by *Dracophyllum traversii* and *Phyllocladus alpinus* (group III and IV). *Olearia "macrodonta"* reveals a slightly larger ecological amplitude and single individuals can occasionally invade the above mentioned forest associations. *Olearia "macrodonta"* can develop three different growth habits, the erect tree and the erect shrub habit like

Olearia ilicifolia, and what can be described as a decumbent treelet with a stem diameter of up to 20cm. This feature may have been inherited from the *Olearia arborescens* parentage. It is individuals with this particular growth habit that are occasionally found within the *Dracophyllum traversii/Phyllocladus alpinus* subalpine low forest associations. Presumably, the decumbent growth habit allows the successful exploitation of nearby canopy gaps downslope after seedling establishment at suitable sites. The same growth habit enables *Senecio bennettii* to grow in dense subalpine forest.

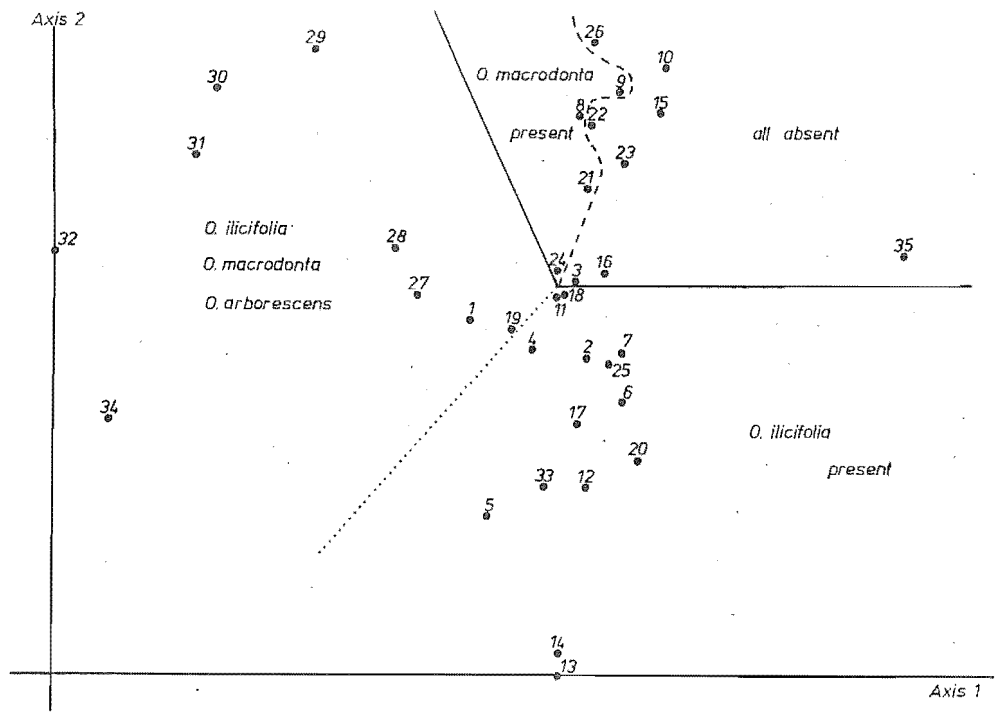

Figure 85. Polar ordination diagram showing the distribution of *Olearia ilicifolia*, *O.arborescens* and *O."macrodonta"*.

Senecio bennettii is present in all types of vegetation, it is usually abundant to common and is only less prominent in the *Hoheria glabrata/Olearia ilicifolia* forest associations at sites with high soil fertility.

Figure 86 shows the distribution of *Dracophyllum traversii* throughout the sample plots. *Dracophyllum* is prominent in the subalpine low forest associations in group III and IV and also in group V which constitutes the successional scrub. Only occasional saplings and poles occur in the stands of group II, and *Dracophyllum* is entirely absent from the fertile sites (group I) and at higher altitudes (group VI).

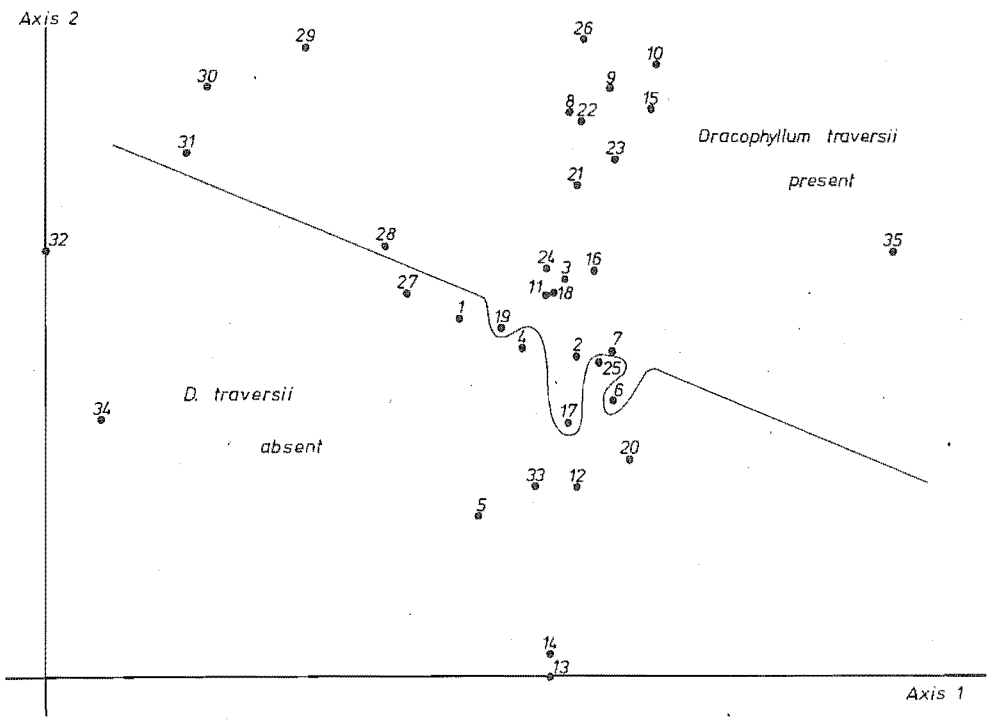

Figure 86. Polar ordination diagram showing presence and absence of *Dracophyllum traversii*.

Figure 87 shows a clear cut partitioning of the available sites between *Dracophyllum traversii*, *Olearia ilicifolia* and *Hoheria glabrata*. *Senecio bennettii* occurs throughout but its limited presence at the sites with high soil fertility corresponds with the absence of *Dracophyllum traversii*. Both *Olearia ilicifolia* and *Senecio bennettii* occur as shrubs above treeline.

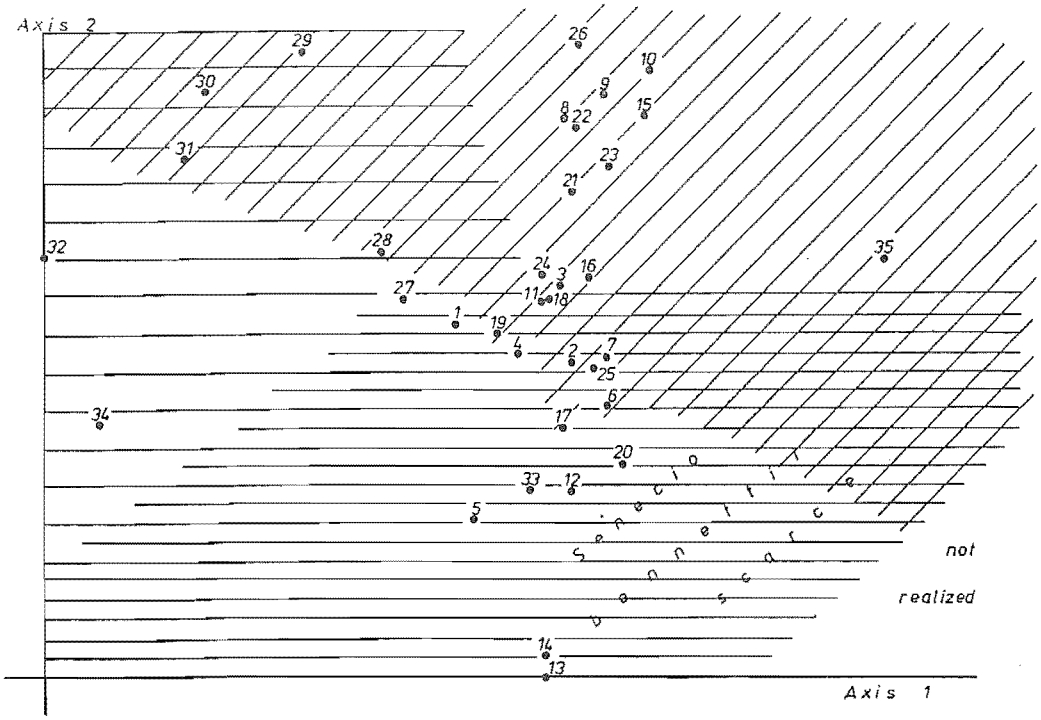

Figure 87. Polar ordination diagram with distribution of the four subject species superimposed by different hatching. Horizontal hatching: *Olearia* and *Hoheria* present; double spaced horizontal hatching: *Olearia* present; transversal hatching: *Dracophyllum* present. *Senecio* is present throughout.

Availability of soil nutrients, usually directly related to the relative maturity of the soil profile, is supposed to be the most important factor determining the floristic composition of the investigated subalpine forest stands. With regard to the four subject species, *Hoheria glabrata* represents the one extreme, it flourishes best on recently disturbed sites with high soil fertility. High growth rates and the relative "luxury" of deciduousness with subsequent rapid decomposition and loss of nutrients by accelerated leaching of the litter can be afforded because lost mineral nutrients can be readily replaced by current uptake from the soil solu-

tion. On precarious sites, where disturbance processes (flooding, rockfalls, avalanches) are recurrent, the highly developed ability of vegetative regeneration ensures the survival of *Hoheria* even after severe damage to the trees.

On sites with slightly lower soil fertility and/or a lower incidence of disturbance *Olearia ilicifolia* increasingly assumes co-dominance with *Hoheria glabrata*. *Olearia* is more conservative with regard to its nutrient cycle, growth rates are lower compared with *Hoheria* and the foliage is retained for slightly more than one year; decomposition of the litter is slower, too.

The A-horizon of the soil under *Hoheria glabrata* forest at HGF contains the highest amounts of total nitrogen and total phosphorus. The A-horizons of the soils under mixed *Hoheria/Olearia* forest at OTR and PLC have less N and P, but higher concentrations of exchangeable K than HGF.

Senecio bennettii cannot be readily compared with the two former species because of its different architecture as a shrub. *Senecio* shows less wood and shoot growth but more leaf area growth per shoot than *Olearia*. Though *Senecio* shrubs occur throughout all of the recorded stands, the species is more prominent in forest and scrub of the transitional and late successional associations where soils are more mature and fertility has declined after more and more mineral nutrients have been leached or become unavailable.

The first young *Dracophyllum traversii* individuals appear in the mentioned transitional associations (group II) but older trees are typical and more numerous on sites with mature and podzolized soil profiles. *Dracophyllum traversii* has comparatively small growth rates of wood increment and

shoot extension. Litterfall is sparing, decomposition of the nutrient poor litter very slow. This tends to ensure a closed nutrient cycle with the best possible conservation of nutrients at sites with nutrient deficient soils. Parsons (1968) elucidated the significance of growth rate comparisons and stressed the relationship of slow growth rates and infertile soils. Low growth rates are viewed as an adaptive strategy to ensure slow but sustained growth of plants at sites with low soil fertility; current uptake of minerals from the soil will not exceed the rate of release of ions from unavailable forms into the soil solution. Species with inherently higher growth rates will tend to outstrip these resources and are unsuited to grow on these sites. The outlined relationships are confirmed by the findings of the present study and it can be added that low soil fertility and growth rates are also correlated with low element concentrations in plant tissues of the respective species.

16. DISTRIBUTION OF THE FOUR SUBJECT SPECIES WITHIN ARTHUR'S PASS NATIONAL PARK AND ADJACENT AREAS

(1) *Hoheria glabrata* and *Olearia ilicifolia*

Though very common trees in subalpine environments, *Hoheria glabrata* and *Olearia ilicifolia* are also important members of early successional forest on river terraces at relatively low altitudes in Westland (e.g. Cockayne et al, 1932). Frequent flooding, erosion of riverbanks and deposition of gravel creates suitable ground for the two species and dispersal of their seeds by running water may be an im-

portant means to ensure exploitation of these niches. In mountain lands various kinds of disturbance, e.g. flooding, slips, rockfalls, avalanches, create more widespread and diverse habitats for species like *Hoheria glabrata* and *Olearia ilicifolia* and there is reduced competition from other early successional species like *Aristotelia serrata, Carpodetus serratus, Coriaria arborea*, etc., which do not ascend to such high altitudes.

In the vicinity of Arthur's Pass patches of almost pure *Hoheria glabrata* low forest occur in the Pegleg Creek Gorge up to an altitude of 900-950m. Conspicuous groves are found at the source of the creek that originates at Kellys Hill and in the upper Kellys Creek catchment. *Hoheria glabrata* is widespread in the Camp Creek catchment, Alexander Range, but is far less common in the mountains west of the Alpine Fault. There is one grove of *Hoheria* at the eastern slope of Mount French, Hohonu Range, but the species was not encountered at Mount Te Kinga.

Olearia ilicifolia is a common tree or shrub throughout the Southern Alps, but only two shrubby individuals were seen in a gully at Mount Te Kinga and none were noticed in the vicinity of Mount French. At Pegleg Creek the altitudinal limit is met at 950m or slightly more; shrubby individuals ascend to 1000m.

Both *Hoheria* and *Olearia* are still be found up to a few kilometres east of the Main Divide at Arthur's Pass, Goat Pass and Walker Pass, but are rarely encountered S of the Waimakariri River. An isolated population is present on Banks Peninsula.

The mountains west of the Alpine Fault are not affec-

ted by the uplift of the Southern Alps and processes of erosion are less pronounced. Granite, the parent rock, shows different weathering forms and is more resistant; the typical talus fans encountered in the Alps proper, are missing. Snow cover is unimportant and avalanches are probably unknown here. Thus suitable habitats for *Hoheria* and *Olearia* and a number of other early successional species are much reduced, and seed sources are usually too distant.

The most common trees and shrubs of the subalpine belt of these mountains are *Dacrydium biforme, Olearia colensoi* and *Dracophyllum longifolium*.

(2) *Senecio bennettii*

Senecio bennettii is particularly abundant at Arthur's Pass but is also well represented in the subalpine scrub above timberline in the Rolleston River catchment and on the Kelly Range. Low browsing pressure may have enabled the species to maintain higher numbers in these areas (Wardle and Hayward, 1970). At both sides of Goat Pass and at Walker Pass *Senecio bennettii* is only present as small undergrowth shrubs in dense subalpine scrub and it is supposed that deer and chamois browsing may have contributed to its suppression.

Only one seedling of *Senecio bennettii* was noted alongside the track to Mount French and the species may be absent from Mount Te Kinga.

The altitudinal limit of *Senecio bennettii* scrub at Arthur's Pass is approximately 1000m but single individuals were encountered up to 1100m.

(3) *Dracophyllum traversii*

Dracophyllum traversii, too, is remarkably abundant

Figure 88. Subalpine low forest of *Dacrydium biforme* at the northern slopes of Mount French, Hohonu Range.

Figure 89. Scattered scrub of *Olearia colensoi* above timberline at Mount French, Hohonu Range. Note the typical growth habit (spherical shrubs).

in the subalpine low forest at Pegleg Flat when compared with other locations in the vicinity. At Arthur's Pass (922m) it crosses the Main Divide and scattered individuals occur in the beech forest south of the Pass. *Dracophyllum traversii* is most common on the steep slopes of the Pegleg Creek Gorge where it ascends up to 950m or more. The last specimens of this population grow in the subalpine scrub south of Lake Misery at an altitude of 920-930m, the saddle itself seems to be too exposed to allow for the growth of woody plants other than patches of low scrub, or regeneration after the fires is exceedingly slow. A small but healthy population of *Dracophyllum traversii* is found in the gorge of the Upper Twin Creek that also harbours an outlier of beech forest. Further south a number of mainly young trees is growing in openings of the beech forest in the upper Bealey Valley at an altitude of about 950m and occasional trees can be found along the Bridal Veil walking track due north of the Arthur's Pass settlement. Further spread south, i.e., away from the Main Divide, seems to be checked by the sudden decline in precipitation. Burrows (1969) noted that the distribution of *Dracophyllum traversii* at Arthur's Pass National Park is related to the position of the 2500mm isohyet.

In the Rolleston River catchment *Dracophyllum* is a member of the upper montane to subalpine forest and shares co-dominance with *Libocedrus bidwillii*, *Podocarpus hallii*, and *Metrosideros umbellata*.

Dracophyllum traversii is absent on the SE side of the Main Divide at Goat Pass (1076m) and Walker Pass (1105m). North of Goat Pass the first individuals were encountered at the confluence of the Pass creek and the Deception River at

an altitude of approximately 940m, and at Walker Pass a group of trees ascends to about 1000m at the confluence of the creeks originating at Tarn Col and Amber Col.

Dracophyllum traversii is common at Camp Creek, Alexander Range, where it is usually associated with *Olearia lacunosa*. At Mount French and at Mount Te Kinga, but also at the western side of Goat Hill, Otira, the subalpine vegetation is dominated by *Dacrydium biforme* forest and scrub, and patches of *Dracophyllum traversii* are restricted to pockets between the montane broadleaf forest and the *Dacrydium biforme* forest.

Dracophyllum traversii stands are normally situated at the head of valleys or depressions where the soils will be deeper and better drained.

Throughout the Arthur's Pass region 950m seems a good approximation for the upper altitudinal limit of *Dracophyllum traversii*. In the mountains around Lake Brunner, North Westland, the species ascends to 1000m or more, possibly as a result of the still milder climate.

Though scattered individuals of *Dracophyllum traversii* seem to occur in several places SE of the Main Divide (refer to map in Burrows, 1969), only the Arthur's Pass population has spread to some extent to the south. This was possible because the altitude of the Pass (922m) is below the upper altitudinal limit of the species and allowed a transalpine dispersal. The higher Goat Pass (1076m) and Walker Pass (1105m), for example, seem to have acted as effective dispersal barriers. Transalpine spread of *Dracophyllum traversii* into the upper Hurunui catchment was also possible at Harper Pass (963m)(C.J.Burrows, pers.comm.).

C H A P T E R VII

EXPERIMENTAL SEED GERMINATION, SEEDLING GROWTH TRIALS AND FOLIAR ANALYSIS

1. MATERIAL AND METHODS

(1) Seed germination experiments

Several thousand seeds of all four species were collected during April and May, 1982, and additional collections were made in the two following seasons. Usually, complete clusters, corymbs or panicles were sampled. The seeds were air-dried for 2-3 days and then stored in airtight plastic bags at 4°C. By this type of storage it proved possible to keep the seeds viable for at least 18 months while preventing untimely germination. Samples of the seeds were counted and the percentage of filled, empty and predated seeds was calculated.

For the germination trials, 25-100 seeds (depending on particular seed-size) were placed on moist filter paper in petri dishes (Whatman, grade 181, 9cm diameter - this type of filter paper is relatively thick, of rough texture and soaks up considerable amounts of water). The petri dishes were then exposed in a growth chamber at either 20°C or 25°C, or at room temperature, keeping the filter paper moist throughout the experiment. The petri dishes were checked each day and germinated seeds (emerged radicle) were counted and removed.

Seed lots showing only poor germination in these pilot trials were submitted to chilling pretreatment. To prevent excessive growth of mould during the several weeks to months

of cold storage, the seeds were briefly (30s) washed with a commercial mould cleanser, then rinsed in distilled water and placed on filter paper in petri dishes. For the chilling pre-treatment the petri dishes were placed to a cold-room (4°C) and the seeds kept moist all the time. From time to time, 50 seeds were removed for germination tests and the effect of the chilling noted.

Seeds of *Senecio bennettii* had to have their seeds coats cut with a razorblade to ensure immediate germination.

(2) Seedling growth under greenhouse conditions

A number of controlled growth trials were planned in order to observe and quantify the growth response of the different species to varying levels of light and nutrient supply. The trials were run in a ventilated glasshouse with automatic watering. The system was timed to water four times a day from late morning to afternoon in order to keep the otherwise high day temperatures down and prevent drought effects. The seedlings were raised in plastic berry punnets (225 x 160 x 70mm) filled with a soilless potting mix consisting of bark, sphagnum, punga dust, sand and trace elements. Increasing amounts of slow release fertilizer pellets (NPK = 15:5.2:12.5) were added for the respective trials. Wooden frames with a single, double and triple layer of shading cloth were used to simulate decreasing insolation. One layer of the employed shading cloth reduces the original unobstructed light intensity to about one third, each successive layer to about half the previous level. Respective light values, as calculated from repeated measurements with a luxmeter, are 38.6±4.9% (S1), 18.3±4.2% (S2) and 7.5±1.4% (S3) of the unobstructed light intensity.

(3) Experimental design of the foliar analysis

(a) Nitrogen. The nitrogen contents of ovendried (105°C) and ground leaves, litter, shoots, wood, bark, flowers and seeds were determined using the microkjeldahl method as described in chapter IV. Two replicates of 0.1g of plant material were used in each trial.

(b) Determination of P, K, and Ca. Two replicates of 1g of plant material were weighed into porcelain crucibles with 3ml of 30% $Mg(NO_3)_2 \times 6H_2O$ solution and sufficient water to wet the sample added. The sample was heated to dryness and then transferred to a muffle furnace and ashed at 550°C for 3h. After cooling the ash was dissolved in 5ml 2N HCl, filtered (Whatman No.42 paper) and diluted to 100ml. K and Ca were determined on an EEL flame photometer and P was measured as described in chapter IV using an aliquot of 0.5ml solution.

2. RESULTS OF THE SEED GERMINATION EXPERIMENTS

(1) Viability of the harvested seeds

Table 26 gives the mean percentages of filled, empty and predated seeds (achenes) of individually counted samples. In *Hoheria* and *Dracophyllum* there is a clear cut difference in seed size between filled and undeveloped seeds. This is less obvious in *Senecio* and sometimes rather uncertain for *Olearia ilicifolia*. During a germination test for this species, using only "undeveloped" achenes, 2% of these germinated. It is not known whether any of the "filled" category lacked a developed seed. Most of the predated achenes were filled but empty ones were also destroyed by the predators.

Most seeds of *Hoheria glabrata* were sound (65.4%,

Table 26: Viability of harvested seeds.

	filled	empty	predated	total
Hoheria	4765 (65.4%)	1919 (26.4%)	597 (8.2%)	7281
Olearia	351 (20.8%)	1116 (66.0%)	224 (13.2%)	1691
Senecio	4204 (39.5%)	5002 (47.0%)	1431 (13.5%)	10637
Dracophyllum	400 (3.0%)	12992 (97.0%)	2 (.01%)	13394

extremes 43.9% and 81.6%) another 8.2% were damaged or destroyed. The remaining 26.4% (13.7-40.3%) were undeveloped, i.e., the coccus contained only a rudimentary seed. Only 20.8% (15.9-40.8%) of all counted *Olearia ilicifolia* achenes contained sound seeds, 13.2% (9.9-13.8%) were predated and 66.0% (47.6-70.3%) were empty. The respective data for *Senecio bennettii* were 39.5% (12.9-53.8%) filled, 13.5% (0.5-38.4%) predated and 47.0% (28.3-79.0%) empty achenes. Similar predation rates in both composites may indicate that they share the same predator (see section 13, chapter VI). The vast majority (97.0%) of all *Dracophyllum traversii* seeds abort at an early stage of development. A single pentamerous capsule contains an average of 335±12.7 seeds of which only 10.0±1.55 are grown to full size, only very few of these are predated (approximately 0.01%).

(2) General conditions of germination

Without special pretreatment only the achenes of the two composites show any noticeable germination. The same was found for achenes of other composites from the same locality. *Olearia avicenniaefolia, O.nummularifolia, O.arborescens,* and the member of the Scrophulariaceae *Hebe salicifolia,* all show fast (starting after 4 days) and almost total germination. Germination of *Hoheria glabrata* and *Dracophyllum traversii* was only very sporadic. Germination of *Hoheria* improved

after three weeks of cold storage at 4°C and stratification was complete after a minimum of six weeks. *Dracophyllum traversii* seeds possibly need a more extended period of stratification; optimal germination was achieved after nine weeks storage at 4°C.

(3) Germination temperature

The two composites and *Hoheria* germinated under growth cabinet conditions (20-25°C, 16h artificial light), the higher temperature positively affecting the germination time. Imbibed *Hoheria* seeds that were kept constantly at 4°C all germinated in the dark of the cold room after 6-7 months. *Dracophyllum traversii* seeds show very poor to no germination under constant temperature even after stratification pretreatment. It was found that even unstratified seeds showed some, though sporadic, germination at room temperature, i.e., approximately 20°C daytime and about 15°C nighttime temperature. In one germination trial, stratified seeds were exposed to either constant 25°C and room temperature. After four weeks more than half of the room temperature trial but none of the 25°C trial had germinated. The seeds were then transferred from 25°C to room temperature, but only few of them germinated. Most of the seeds were probably dead after exhausting their energy reserves through high respiration rates.

(4) Light requirements for germination

Germination of *Hoheria glabrata* appears to be independent of light (see above). *Olearia ilicifolia* seeds soon die when kept in the dark at suitable temperatures. The same applies for *Senecio bennettii* though one seed germinated in

the dark. Light is also essential for the germination of *Dracophyllum traversii* seeds.

(5) Other factors

Germination of *Senecio bennettii* is always more or less sporadic and stretches over a considerable period of time. Therefore, additional treatments were applied in order to speed up the germination process. Rinsing in tap water for 20h and 40h failed to improve germination. After the achenes (fruit wall plus seed coat) had been slit with a razorblade, response was immediate and almost complete germination was achieved within 3-13 days, though a number of seedlings were damaged in the process and did not develop normally. It is therefore assumed that the fruit wall and/or seed coat delays germination until its tissue is sufficiently weakened, probably during the process of increasing decay.

(6) Rate of germination

After the optimum germination conditions had been established germination trials were carried out on a larger scale to investigate the rates of germination. For these experiments *Hoheria* and *Dracophyllum* seeds were adequately stratified as a pretreatment. The composite achenes were kept moist at $4^{o}C$ for three days prior to exposure to ensure they were fully imbibed (as were the stratified seeds) at the start of the trials. *Hoheria, Olearia* and *Senecio* seeds were germinated in a growth cabinet at constant $20^{o}C$ and *Dracophyllum* seeds at room temperature. The results are shown in figure 90.

Germination (radicle emergence) of *Hoheria glabrata*

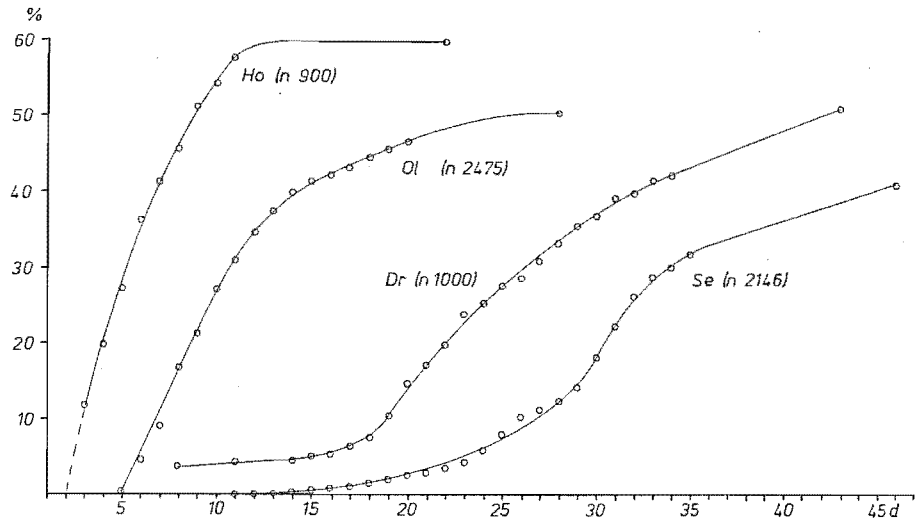

Figure 90. Rates of seed germination of the four subject species; see text for germination conditions and pretreatments.

started on the third day after exposure, 50% germination was approached on the ninth day, but then the rate of germination abruptly declined on day 11-12. The experiment was stopped after 22 days with 59.8% of all seeds germinated.

A few *Olearia ilicifolia* achenes had already germinated on the fifth day of exposure; initial germination rates were kept until about day 12 (34.7%) but then declined, 50% germination was reached after approximately 25 days.

The first *Senecio bennettii* achene germinated after 11 days, more after 13 days. Germination rates slowly increased to a maximum after 29-32 days then declined but probably remained constant for some time. The experiment was discontinued after 46 days when 41.1% of the achenes had germinated. 50% germination may be expected after about 55 days.

Germination of *Dracophyllum traversii* was first checked on the eighth day of exposure, by this time 3.7% of the seeds had - unlike in earlier trials (13-18-21 days) -

already germinated and may have started to do so as early as day 5 after exposure. Subsequent germination was slow until the 18th day (7.6%) when rates increased considerably. Earlier germination can probably be accounted for as sporadic germination of some seeds with faulty seed coats and was not encountered in previous trials which were on a smaller scale. Rates gradually declined and 50% germination was probably achieved after 42 days. The final germination was 51.1% after 43 days when the experiment was discontinued.

Both *Hoheria* and *Olearia* reveal only a short time lag between exposure and first germination, high initial germination rates and a definite end after which hardly any further germination occurs. *Senecio* and *Dracophyllum* need a longer incubation time before germination starts, rates of germination are slower and germination will continue at least sporadically for a long time the exact span of which could not be covered during the experiment.

3. SEEDLING GROWTH EXPERIMENTS UNDER GLASSHOUSE CONDITIONS

(1) Experiment I

Thirty germinated seeds were placed at equal distances from each other in prepared holes of about 10mm depth and were covered with the substrate. 0, 0.1, 0.3 or 1.0g of the slow release fertilizer were added and the containers placed either in full sunlight or under a single or double layer of shading cloth. Three replicates of each treatment were prepared. The maximum amount of fertilizer was derived from the recommendations for horticultural purposes and from an experimental design by Parrish and Bazzaz (1982). After two months the fertilizer application was repeated. After two

more months the total plants were harvested, cleaned, oven-dried and their dry weight determined.

Though *Dracophyllum traversii* seeds germinated freely under the stated favourable conditions the young seedlings always died after a few days and it was not possible to establish them for further growth trials.

Table 27: Dry weight of seedlings of experiment I.

	fert. / trial	light level L	S1	S2
Hoheria	0.0g	17.6±4.1	25.8±6.4	21.4±5.3 mg
	0.1g	20.6±4.8	- - - -	- - - - mg
	0.3g	36.5±8.1	- - - -	- - - - mg
	1.0g	88.5±19.7	66.9±13.3	71.2±14.2mg
Olearia	0.0g	1.6	- - - -	2.1 mg
	0.1g	1.8	- - - -	- - - - mg
	0.3g	3.9	- - - -	- - - - mg
	1.0g	4.4	40.0±16.3	30.8±9.1 mg
Senecio	0.0g	4.5	5.0	- - - - mg
	0.1g	4.6	- - - -	- - - - mg
	0.3g	4.75	- - - -	- - - - mg
	1.0g	6.3	20.1±5.5	15.8±5.3 mg

Hoheria glabrata seedlings showed the highest dry weight of the three species in any of the trials. The maximum dry weight was gained in the L,1.0 trial (88.5±19.7mg/plant) but the difference of the mean is only significant at the 10% level when compared with trial S1,1.0. Comparison of the means of the L,1.0 versus S2,1.0 and S1,1.0 versus S2,1.0 trials give insignificant results.

Dry weight of *Olearia ilicifolia* seedlings was highest in the S1,1.0 trial (40.0±16.3mg/plant), the difference of the means S1,1.0 and S2,1.0 is insignificant.

Senecio bennettii also attains maximum dry weight in the S1,1.0 trial (20.1±5.5mg/plant) but the difference to the S2,1.0 trial is insignificant as well.

The unshaded plants received full sunlight but also suffered from temporary drought and high temperatures (at times exceeding 30°C) which stunted their growth and biomass gain. Effects of fertilizer in the L-trials were only on a minor scale in *Olearia* and *Senecio*, but better expressed in *Hoheria*. Shading did not significantly increase dry weight of unfertilized plants except for the *Hoheria* L,0.0 and S1,0.0 trials, where the difference of the means is significant at the 2% level.

(2) Experiment II

As the first seedling growth experiment did not reveal any negative response to the 1.0g fertilizer doses (this was found to be the case for certain late successional species by Parrish and Bazzaz, 1982), the amount was increased to 3.0g in the second experiment; an additional triple layer of shading cloth was introduced as well. This time only 20 germinated seeds were placed in each container. Plants were harvested as before after three months.

Hoheria gained maximum dry weight in the S2,3.0 trial (605.5±187.5mg/plant), followed by S3,3.0 (146.5±29mg/plant) and S1,3.0 (134.7±84.2mg/plant). The L,1.0, S1,1.0 and S2,1.0 trials can be directly compared with the respective trials of the first experiment which differ in total duration and seedling density (table 29). The S1,1.0 and S2,1.0 trials reached

Table 28: Dry weight of seedlings of experiment II.

	fert. trial	light level L	S1	S2	S3	
Ho.	1.0g	8.2±1.8	29.0±13.1	30.9±9.4	25.9±8.5	mg
Ho.	3.0g	27.9±51.2	134.7±84.2	605.5±187.5	146.5±29.0	mg
Ol.	1.0g	10.0±4.3	18.5±20.4	143.4±81.2	10.3±23.6	mg
Ol.	3.0g	96.6±98.8	146.9±59.9	244.6±88.1	25.4±6.1	mg
Se.	1.0g	20.3±23.4	14.1±13.5	8.2±2.5	5.4±1.6	mg
Se.	3.0g	24.0±8.3	52.7±15.0	57.9±18.5	14.8±5.3	mg

Table 29: Comparison of mean dry weights of *Hoheria* seedlings of the 1.0g trials of experiments I and II.

	L	S1	S2	
experiment I	88.5±19.7	66.9±13.3	71.2±14.2	mg
experiment II	8.2±1.8	29.0±13.1	30.9±9.4	mg
% of exp. I	9.3%	43.3%	43.4%	

43.3 and 43.4%, respectively, of the dry weight of the previous experiments but L,1.0 attained only 9.3% which may be due to a profuse cover of liverworts that developed in the respective trays.

Mean differences between the S1,1.0, S2,1.0 and S3,1.0 trials are insignificant, i.e., fertilization is supposed to be the limiting factor rather than light intensity.

Olearia also attained the highest dry weight in the S2,3.0 trial (244.6±88.1mg/plant) followed by S1,3.0 (146.9± 59.9mg/plant) and S2,1.0 (143.4±81.2mg/plant). The L,3.0 trial is only represented by five individuals which gained a mean dry weight of 96.6±98.8mg. Results do not compare with the trials of the first experiment, dry weight of the L,1.0

and S2,1.0 trials was larger, dry weight in the S1,1.0 trial smaller (46.3%) in relation to the first growth experiment. The plants of the S3,1.0 and S3,3.0 trials showed a much reduced dry weight, their leaves remained unsclerotinized and they produced only very few roots.

Senecio bennettii, too, gained maximum dry weight in the S2,3.0 trial (57.9±18.5mg/plant) followed by trials S1,3.0 (52.7±15.0mg/plant) and L,3.0 (24.0±8.3mg/plant). The four trials with 1.0g of fertilizer show a slight but insignificant decline in dry weight with increasing shading, only the difference of the means between S2,1.0 and S3,1.0 is significant at the 0.1% level.

All three species appear to be shade tolerant if not shade loving. Exposure to full sunlight (combined with high temperatures and low humidity levels) tend to decrease total plant dry weight. All species do considerably better under the S1 cover (light intensity reduced to 38.6%) but maximum dry weight is only gained under the double layer of shading cloth (18.3% of unobstructed light intensity). There is a sudden decline in dry weight under the S3 cover (7.5% of the unobstructed intensity) when mean dry weight falls abruptly to values lower than those of the L trials (*Olearia* and *Senecio*) but comparable to S1 in *Hoheria*, which is generally less affected by the environmental conditions. NPK-fertilization always increased yield. Even when doses of 3g per tray were applied no damage by oversaturation was caused in the plants.

(3) Experiment III

Another set of growth trials was prepared using two natural substrates. One was coarse sand, derived from grey-

wacke. This sand was thought to resemble closely the substrate of the early successional stages on newly deposited river banks, talus fans and slips. At the other extreme, the A-horizon of soils under mature subalpine low forest at Pegleg Flat was sampled. The soil was screened through a 2mm mesh and sterilized by heat. Polystyrene seedling trays were used to avoid competition for root space and nutrients between individuals. The trays were kept under a single layer of shading cloth to prevent excessive insolation. Two or three seeds (after chilling pretreatment) were placed in each section of the tray. Germination was noted and plants were harvested after three months and their dry weight was determined.

Table 30: Germination of seeds on natural substrates.

	Hoheria		*Olearia*		*Senecio*	
	hum.	sand	hum.	sand	hum.	sand
no. seeds sown	56	56	56	56	84	84
no. seedlings	32	44	38	46	62	69
% of total	57	79	68	82	74	82

Table 31: Seedling growth on different natural substrates.

	Hoheria	*Olearia*	*Senecio*	
humus	39.2±15.0	33.4±12.8	11.0±2.6	mg/seedling
sand	29.4±4.1	4.8±1.4	1.6±0.2	mg/seedling

Results of growth experiment III are given in tables 30 and 31. The total number of seedlings germinated from seeds seems to be higher on the sandy substrate for all three species, better drainage and hence, oxygen supply of the seeds may be a possible explanation. Total dry weight of the seedlings was considerably reduced on sand which lacks nitrogen

and is low in other nutrients, too. Growth of *Hoheria* was less reduced, probably because of the initially higher nutrient reserves of the larger seeds.

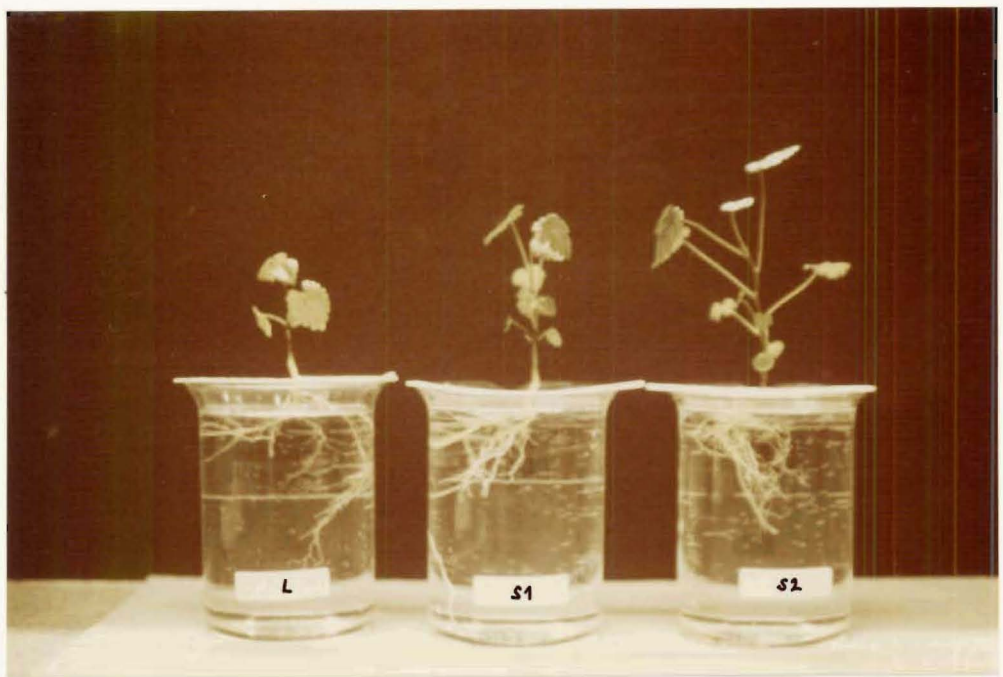

Figure 91. Effect of shading on the growth of *Hoheria glabrata* seedlings. Individuals are of representative size.

4. CHEMICAL ANALYSES OF PLANT TISSUES OF THE FOUR SPECIES

(1) General remarks

Table 32 gives the percentages by weight (oven dry weight, 105°C) of the four major mineral nutrients N, P, K, and Ca that were determined in samples of current season's foliage, one year old leaves and recently shed leaves collected from the ground. The respective element contents of one and two seasons old shoots, wood and bark samples, and flowers and seeds were determined as well.

Hoheria was found to have the highest concentration of all the four elements (N,P,K,Ca) in any of its tissues that

Table 32: Concentration of N, P, K, and Ca in different tissues of the four subject species

	n i t r o g e n				p h o s p h o r u s				p o t a s s i u m				c a l c i u m				
	Ho	*Ol*	*Se*	*Dr*	*Ho*	*Ol*	*Se*	*Dr*	*Ho*	*Ol*	*Se*	*Dr*	*Ho*	*Ol*	*Se*	*Dr*	
fol.1	2.66	1.39	1.51	0.89	0.23	0.14	0.22	0.06	2.21	1.24	1.65	0.27	4.31	0.60	0.58	0.71	%
fol.2	- -	1.03	1.05	0.78	- -	0.09	0.13	0.045	- -	0.78	1.07	0.20	- -	1.15	1.67	0.86	%
litt.	1.03	0.67	0.47	0.37	0.10	0.04	0.06	0.016	0.70	0.44	0.65	0.09	5.09	1.35	1.82	1.04	%
sht.1	1.88	0.84	0.94	- -	0.22	0.20	0.18	- -	1.45	1.56	1.58	- -	1.62	0.53	0.45	- -	%
sht.2	- -	0.93	0.86	- -	- -	0.15	0.14	- -	- -	1.20	1.06	- -	- -	0.45	0.36	- -	%
wood	0.45	0.30	0.25	0.27	0.07	0.05	0.02	0.01	0.39	0.15	0.20	0.12	0.68	0.14	0.14	0.18	%
bark	1.47	0.60	0.57	0.35	- -	0.05	0.02	0.005	- -	0.04	0.08	0.01	- -	0.75	1.12	0.21	%
lf-sc.	- -	- -	- -	0.50	- -	- -	- -	0.02	- -	- -	- -	0.04	- -	- -	- -	6.98	%
flower	2.35	1.05	0.51	0.70	0.38	0.08	0.09	0.03	3.32	0.80	1.70	0.12	0.76	0.79	0.38	0.36	%
seeds	4.48	1.82	3.03	3.99	0.63	0.31	0.52	0.68	0.74	0.45	1.02	0.40	0.36	0.84	0.29	0.92	%

were investigated. *Hoheria* exceeds the respective *Olearia* data for most leaf and litter samples, but the reverse applies in general for shoot, wood and bark samples. Nutrient element contents of *Dracophyllum traversii* tissues are almost always a good deal lower than the respective concentrations for *Hoheria* and the two composites. A notable exception are the samples of the leaf scars which contain an unusual 7% calcium.

Element concentrations are lowest in wood and bark samples but in terms of total biomass they will probably exceed total weight of those in other tissues than wood.

Only those flower parts that make up the bulk of the reproductive organs were considered, to estimate the losses by shedding, i.e., the shed inflorescences of *Hoheria*, corymbs of *Olearia* and panicles of *Senecio* and *Dracophyllum* (parts only). Complete fruits were sampled for *Hoheria*, achenes for the composites and filled seeds for *Dracophyllum*.

(2) Foliar analysis

All leaves in their second season show relative decreases of the N, P, and K concentrations which are still further reduced in the respective litter. An exception is calcium which is relatively concentrated in older leaves and litter. All four elements together constitute 9.4% (*Hoheria*), 3.4% (*Olearia*), 4.0% (*Senecio*) and 1.9% (*Dracophyllum*) of the dry weight of the respective current season's foliage. The high value of *Hoheria* is a result of its deciduous leaves that consists largely of photosynthetic tissue only, foliage of the evergreen species contains larger amounts of supporting tissues (sclerenchyma, phloem fibres). In table 33 element contents of older foliage and litter are expressed as a percentage of the initial concentrations, revealing relative

withdrawal or accumulation of individual elements with increasing age of the leaves. *Hoheria* litter still contains 38.7% of the initial nitrogen concentration of green foliage as well as 43.5% of the phosphorus and 43.0% of the potassium content. *Olearia* appears to be more wasteful with 48.2% of the nitrogen, 49.2% of the potassium, but only 28.6% of the former phosphorus content remaining in its litter. The respective data for *Senecio* are 31.1% N, 27.3% P, and 39.5% K, and for *Dracophyllum* 41.6% N, 26.7% P, and 33.3% K. In the three evergreen species, phosphorus is conspicuously more strongly withdrawn before litterfall. Relative calcium contents of litter are always higher than those of living foliage (e.g. Smith, 1962). This is mainly due to the selective withdrawal of other substances, mostly carbohydrates and N, P, K, with increasing age, whereas Ca (and Mg, Fe and others) are comparatively immobile and thus appear to be relatively accumulated. This may be the case in *Hoheria* with 118% and *Dracophyllum* litter with 146% of the calcium content of young leaves, but the very high values of the composites (*Olearia* 225% and *Senecio* 313%) would rather indicate active accumulation of calcium in ageing foliage.

Table 33: Element content of old leaves and litter, expressed as a percentage of the concentration of current season leaves.

	1 year old foliage				recent litter			
	N	P	K	Ca	N	P	K	Ca
Hoheria	- -	- -	- -	- - -	38.7	43.5	43.0	118.1 %
Olearia	74.1	64.3	62.9	191.7	48.2	28.6	49.2	225.0 %
Senecio	69.5	59.1	63.6	286.0	31.1	27.3	39.5	313.0 %
Dracophylm.	87.6	75.0	74.1	121.0	41.6	26.7	33.3	146.0 %

Table 34: Ratios of the four element contents based on N=1.

	current foliage				1 year old foliage				recent litter			
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Ho.	1:	0.09:	0.83:	1.62	+	-	-	-	1:	0.10:	0.68:	4.94
Ol.	1:	0.10:	0.89:	0.43	1:	0.09:	0.76:	1.12	1:	0.48:	0.06:	2.01
Se.	1:	0.15:	1.09:	0.38	1:	0.12:	1.02:	1.59	1:	0.13:	1.38:	3.87
Dr.	1:	0.07:	0.30:	0.80	1:	0.06:	0.26:	1.10	1:	0.04:	0.24:	2.81

Ratios of the four elements in relation to nitrogen are given for leaves of different ages (table 34). Both *Hoheria* and *Olearia* reveal very similar ratios of N:P:K in leaves of the current season (approximately 1: 0.1: 0.85). *Senecio* has relatively higher P and K ratios (1: 0.15: 1.1) and *Dracophyllum* is particularly low in P and K (1: 0.07: 0.3). The respective ratios in litter of *Hoheria* are 1: 0.1: 0.68, and 1: 0.48: 0.06 in *Olearia*. In *Senecio*, both P and K are relatively less strongly withdrawn (1: 0.13: 1.38), the data for *Dracophyllum* are 1: 0.04: 0.24.

(3) Analysis of plants raised in greenhouse trials

Ovendried seedlings (shoots and leaves) of the S1,1.0 trials of experiment I were also analysed for N, P, and K contents, i.e., the nutrient elements that had been applied to the same amount to each of the species. *Hoheria* and *Olearia* were found to have exactly the same N concentration (2.87%), *Senecio* was only slightly lower in N (2.63%). Phosphorus levels varied from 0.50% in *Hoheria* and 0.45% in *Olearia* to 0.33% in *Senecio*, and K levels ranged from 2.30% in *Hoheria* and 2.66% in *Olearia* to 2.22% in *Senecio*. Calcium, which was only present as a trace element in the soilless potting mix, was found to make up 0.40% of the *Hoheria*, 0.53%

Table 35: Analysis of seedlings from fertilized growth trials.

	N	P	K	Ca	
Hoheria	2.87	0.50	2.30	0.40	% of dry weight
Olearia	2.87	0.45	2.66	0.53	% " " "
Senecio	2.63	0.33	2.22	1.18	% " " "

Table 36: Element ratios of field samples compared with those of growth trials.

	field sample N : P : K	growth trial N : P : K
Hoheria	1 : 0.09 : 0.83	1 : 0.17 : 0.80
Olearia	1 : 0.10 : 0.89	1 : 0.16 : 0.93
Senecio	1 : 0.15 : 1.09	1 : 0.13 : 0.84

of the *Olearia* and 1.18% of the *Senecio* dry weight.

N and K contents of the *Hoheria* seedlings were only slightly higher (5-10%) than analysed leaves from the field samples. P was more than double the rate of sampled foliage. N and K were more than twice, P more than three times higher in the *Olearia* seedlings. N was up by 60%, P by 50% and K by 40% in the *Senecio* seedlings compared with field samples. Calcium, on the other hand, was less than 10% of the natural concentration in *Hoheria*, about 90% in *Olearia* but more than 200% in the *Senecio* seedlings.

N:P:K ratios of the experimental plants show that relative P-uptake was slightly increased in *Hoheria* and *Olearia* while relative K-uptake remained nearly constant. Relative uptake of both P and K was reduced in *Senecio*.

(4) Comparison of the results with other data sources

Data for element contents of leaves of north temperate

trees are available for comparison with *Hoheria glabrata*. Tamm (1951) analysed leaf samples of birch (*Betula verrucosa*) for N, P, K, and Ca throughout the growing season. Leaf samples from trees in a moist grwavel pit during mid-season, that can be best compared with *Hoheria*, showed 2.8-3.1% N in birch (2.4-3.2% in *Hoheria*), birch litter contained only 0.8% (*Hoheria* 1.0%). P content of birch leaves was 0.14-0.22% (0.18-0.27%), of litter 0.07-0.08% (0.09-0.11%). K contents do not compare as well, Tamm found 1.4% K (*Hoheria* 2.2%) in living foliage of birch and 0.16% in litter (*Hoheria* 0.7%). The Ca content was only 0.8% compared with 4.3% in *Hoheria*, birch litter had 1.5-1.6% Ca (*Hoheria* 4.6-5.5%).

With reference to the high Ca contents of *Olearia* and *Senecio* litter, Tamm's data for Ca in birch litter always exceeded 200% of the respective content of green foliage, so these values should not be regarded as extraordinary.

As for evergreens, Nordmeyer (1980) gives data for mountain beech foliage from a stand at 1000m altitude in the Craigieburn Range. The contents of 1.67% N, 0.18% P, 0.44% K, and 0.89% Ca are comparable to *Olearia* and *Senecio* element concentrations except for K which is much lower in mountain beech.

C H A P T E R VIII

D I S C U S S I O N

In the course of this chapter various general aspects of the different ecological strategies with reference to the four subject species will be discussed. The relationships between variations in soil fertility and the longevity and chemical composition of the foliage of the respective species, and evidence for environmental control of vegetative and reproductive growth will receive particular attention. Additionally, habitat preferences and ecological characteristics in general will be summarized for each of the four subject species with emphasis on the different modes of regeneration.

1. STRATEGIES OF EVERGREENNESS VERSUS DECIDUOUSNESS

Perhaps the most striking difference with regard to the four subject species is the deciduous habit of *Hoheria glabrata* compared to *Olearia, Senecio* and *Dracophyllum* which are evergreen and retain their leaves for periods of one to five years. A number of scientists have tried to elucidate the ecological implications of evergreenness and deciduousness with particular reference to the nutrient supply of the respective plants (e.g. Monk, 1966; Moore, 1980; Mooney and Gulmon, 1982). Others established a possible relationship between mineral nutrition and leaf longevity of evergreen shrubs (Reader, 1978; Shaver, 1981,1983). So far, the relationships outlined in table 37 have been verified.

The ecological advantage of evergreenness on nutrient deficient and/or seasonally dry sites has been described by

Table 37: Ecological characteristics of evergreen and deciduous trees and shrubs.

	evergreen	deciduous
carbon cost for maintenance and construction of leaf	high	low
photosythetic capacity	low	high
life span of individual leaf	long	short
leaf specific weight	high	low
element concentration	low	high
recycling of nutrients by litterfall and decomposition	gradual (efficient)	short flush (losses)
growth rates	low	high
soil fertility	low	high
preferred habitat	stable	disturbed

Monk (1966) and Moore (1980). A gradual litterfall helps to conserve nutrient elements within the biogeochemical cycle and resources of the soil are not outstripped.

Mooney and Gulmon (1982) demonstrated an inverse relationship between leaf specific weight (dry weight/cm^2) and leaf nitrogen content and the results obtained during the present study fit well into this scheme (figure 92). Leaf longevity is positively related to leaf specific weight and negatively related to leaf nitrogen content. Though Mooney and Gulmon refer to increasing costs for the defense from potential predators in longer living leaves they do not mention that most of the increased dry weight of evergreen leaves is due to the different structure that is necessary for leaves with life expectancies of more than one season. Most deciduous leaves have a simple basic structure, mainly devised for photosynthetic efficiency, i.e., palisade cells,

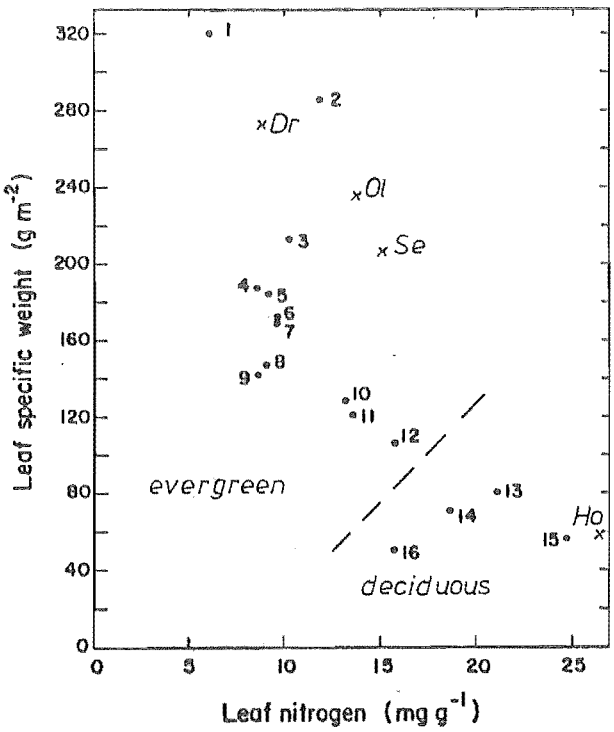

Figure 92. Relationship of leaf specific weight and leaf nitrogen content (after Mooney and Gulmon, 1982). The data for the four subject species of this study have been added (see Mooney and Gulmon, 1982, for full explanation).

spongy parenchyma and a one-layered epidermis; *Hoheria glabrata* falls in this category. There is little supporting tissue (sclerenchyma, phloem fibres) and by the end of the season many leaves appear torn and punctured; they would hardly be of any benefit during a second season. Evergreen leaves in temperate climates must be able to stand environmental stress of different kinds, not only during the growing season but also during the still more unfavourable winter season with frost, snow and high winds. After this they must be able to photosynthetize for at least another season but in some cases for several years more. This is only possible when a good deal of their tissue is made up of sclerenchyma and/or phloem fibres. The extent of photosynthetic tissue will be relatively reduced; sometimes chlorophyll bearing cells make up only about half the volume (e.g. *Olearia, Dracophyllum*). Epidermis and cuticle may be more pronounced and often have several layers. It is therefore not surprising

that leaves with long life expectancies or leaves of extreme environments will tend to have the highest specific weight and, of course, lower leaf nitrogen contents, as N will be relatively diluted by the increasingly built-in structural carbohydrates.

Loveless (1961) found a positive correlation between protein content (which is equivalent to N content) and phosphorus content of leaves and suggested that evergreen sclerophyllous vegetation may be adapted to tolerate low phosphate levels.

With regard to nutrient conservation one of the main questions was the function of the older evergreen leaves for the contribution to plant growth. Hadley and Bliss (1964) found negative net carbon gain in old leaves of *Ledum groenlandicum* (Ericaceae) in an alpine environment and concluded that old leaves serve mainly as nutrient storage organs to allow for faster growth during the short growing season. This view was supported by Shaver (1981,1983) who studied the related *Ledum palustre*. Reader (1978,1980), after work on *Ledum groenlandicum* and two other ericaceous shrubs, suggested that though new growth may in some cases be retarded by removal of older leaves, little translocation of phosphorus and nitrogen from old to new leaves actually takes place. It was, rather, newly synthetized material that was exported from old leaves as they revealed positive net photosynthesis. Mooney and Gulmon (1982) stated that the decreasing but still positive photosynthetic capacity of older leaves is not simply a function of age but an adjustment due to relocation of the carboxylating enzyme from old to new foliage for the sake of greater working efficiency as the older

leaves are increasingly shaded out. Maintaining a high photosynthetic capacity, i.e., enzyme concentration, in old foliage would be a waste of resources as the low light intensity reaching the leaves would be the limiting factor for the photosynthetic rate. Reader (1978) was able to demonstrate that net photosynthetic rate (and N-concentration) decreased with leaf age but that in terms of leaf nitrogen content new and old leaves fixed equal amounts of carbon. Not leaf age per se but the changing environmental conditions for the individual leaf is the cause for declining photosynthetic activity (Mooney and Gulmon, 1982).

The proposals of Reader (1978, 1980) and Shaver (1981, 1983) are based on studies of North American subarctic shrubs growing on nutrient deficient soils and in a climatically severe environment and can therefore not be directly compared with New Zealand evergreen subalpines. The mild climate in the wet western districts of the South Island allows evergreen species to keep up photosynthetic activity to a certain extent throughout the winter. This in itself would provide an ecological advantage even if the leaves would be shed later on without being of further use. Nutrient supply of expanding foliage can, for the most part, probably be met by current uptake from the soil, and nutrient storage would be more likely to be in the sapwood as these arborescent species possess a much higher wood/foliage ratio than the smaller sized subarctic shrubs dealt with by the above mentioned authors. Shading by expanding new foliage resulting in accelerated senescence and subsequent shedding of older leaves as proposed by Mooney and Gulmon (1982) is considered as a more likely cause. As there was considerable variation in

the rate and timing of litterfall during the two observed seasons, it is not supposed that leaf shedding is simply a function of leaf age.

Bussell (1968) whose studies were mainly concerned with the growth and phenology of New Zealand deciduous trees, noted a basic difference between indigenous and northern hemisphere species with regard to environmental control of litterfall. Whereas short daylength is responsible for a contracted autumn litterfall in northern temperate trees, the deciduous *Aristotelia, Fuchsia* and *Hoheria* lost some leaves throughout the growing season though a distinctive peak occurred in autumn. Bussell noted that greenhouse specimens kept some of their foliage throughout the winter but outdoor plants were leafless, and suggested that temperature rather than daylength controls litterfall. The same can be concluded from the occasional remarks on wintergreen *Hoheria glabrata* at lower altitudes in Westland (Cockayne, 1904, 1906) or after warm periods in late autumn (Russell, 1936).

As for evergreens it was found that litterfall and leaf area growth of *Olearia ilicifolia* coincides in timing and is in direct proportion. These facts in themselves do not explain why the older leaves are shed as both causes mentioned above may be responsible. There is, however, some evidence that points towards the shading effect of the expanding foliage as being the more important factor. It was observed that in *Olearia* and *Senecio* often smaller, younger leaves were shed in favour of larger but older ones that were retained for some time longer. If element transfer to the new foliage is the prime cause for leaf shedding, there would be no ready explanation for this preference. On the other

hand, small leaves become most easily completely outshaded by the expanding new foliage and will show a negative net carbon balance, it is therefore an ecological advantage to shed them. Large leaves will usually only become partially shaded, can still maintain a positive carbon balance and enjoy a longer life expectancy. In both composites litterfall also takes place later in the season when it is unrelated to current new growth.

Seasonal variation in leaf area increment is also correlated with the extent of litterfall. In *Olearia ilicifolia* new leaf area was greater in the 1982/83 growing season than the year before and shedding of the old 1981/82 leaves was very pronounced during the period of new growth; all old leaves on control shoots were shed by July/August. In this case more intensive shading by the expanding foliage may have accounted for the accelerated litterfall. In the subsequent 1983/84 season new leaf area growth was considerably less, fewer and smaller leaves were produced. Litterfall was far less pronounced as a result. The smaller number and size of the new leaves cast less shade and would favour a prolonged life expectancy of the old foliage according to the theory of Mooney and Gulmon (1982).

In *Dracophyllum traversii* litterfall is restricted to the growing season and is in direct proportion to new leaf area growth. It can not be ascertained from the present data whether increasing shading or nutrient export is the prime cause for shedding of old leaves, but in this particular instance - leaves are strictly shed according to their age sequence - severing of the leaf traces by increasing wood and bark increment may be a simple answer to the timing of litter-

fall.

Fast growing saplings of all three evergreen species retain more old leaves per shoot than do adult trees. Saplings have higher growth rates both in terms of leaf area and shoot length and the latter, in turn, achieves a wider vertical spacing of individual leaves and mutual shading is kept at a minimum.

As denizens of the subalpine belt these species tend to have slow growth rates, internodes tend to be very short and the foliage is usually crowded into terminal rosettes or almost so, so that mutual shading is likely to be pronounced. The importance of shading is reflected by the close relationship between phyllotaxis and the number of annually produced leaves in the three evergreen species.

2. ENVIRONMENTAL CONTROL OF SEASONAL LEAF AREA GROWTH AND SHOOT GROWTH

Annual amounts of shoot length and leaf area per shoot of all four subject species show considerable variation from year to year and are supposed to be influenced by the climatic conditions prevailing during or prior to the growing season. Four distinct patterns of variation can be recognized over the three observed growing seasons:

1) a maximum in 1982/83 (the coolest season of all) with a decline towards 1981/82 and a more pronounced decline (minimum) in 1983/84, e.g. leaf area in *Olearia*, shoot growth in *Olearia* (distinct at the OTR stand only).

2) a steady decline with a more pronounced drop from 1981/82 to 1982/83, e.g. shoot growth in *Senecio* at HTS, *Olearia* saplings, and most stands of *Hoheria*.

3) a more or less steady decline from 1981/82 to 1983/84, e. g. leaf area in *Senecio*, shoot length in *Senecio* at SCL. 4) increase in leaf area growth from 1982/83 to 1983/84 in *Dracophyllum*.

It is usually assumed that the climatic quality of the growing season, especially in terms of temperature and radiation, is directly related to plant yield. Theoretically, this may be achieved in several ways; 1) variation in the total duration of the growing season as determined by higher or lower than normal temperatures in spring and/or autumn, 2) higher or lower than average temperatures during a growing season of usual duration, 3) in perennial plants the quality of the previous season may be important, too, and have a bearing on the concentration of stored nutrients and the predetermination of the number of leaves in the resting bud.

The growing season 1983/84 commenced earlier and had higher mean summer temperatures than the cooler than normal 1982/83 season (figure 93). However, only the leaf area increment of *Dracophyllum traversii* is positively related to the duration and warmth of the growing season (figure 94).

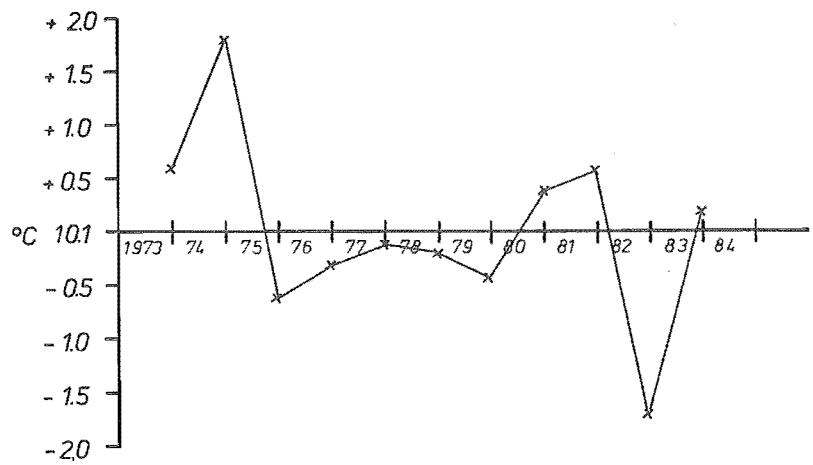

Figure 93. Annual variation of the mean summer temperature (average of mean monthly temperatures from October to March).

In *Olearia ilicifolia* maximum growth rates and total leaf area per shoot were considerably less in 1983/84, in spite of a slightly extended growing season and higher mean temperatures during peak growth rates (1°C above the 1982/83 mean). Figure 94 shows average daily increment rates of leaf area expressed as unit area per day for the three evergreens. The data were interpolated from the leaf area growth diagrams (chapter VI, section 7) on the basis of five day periods.

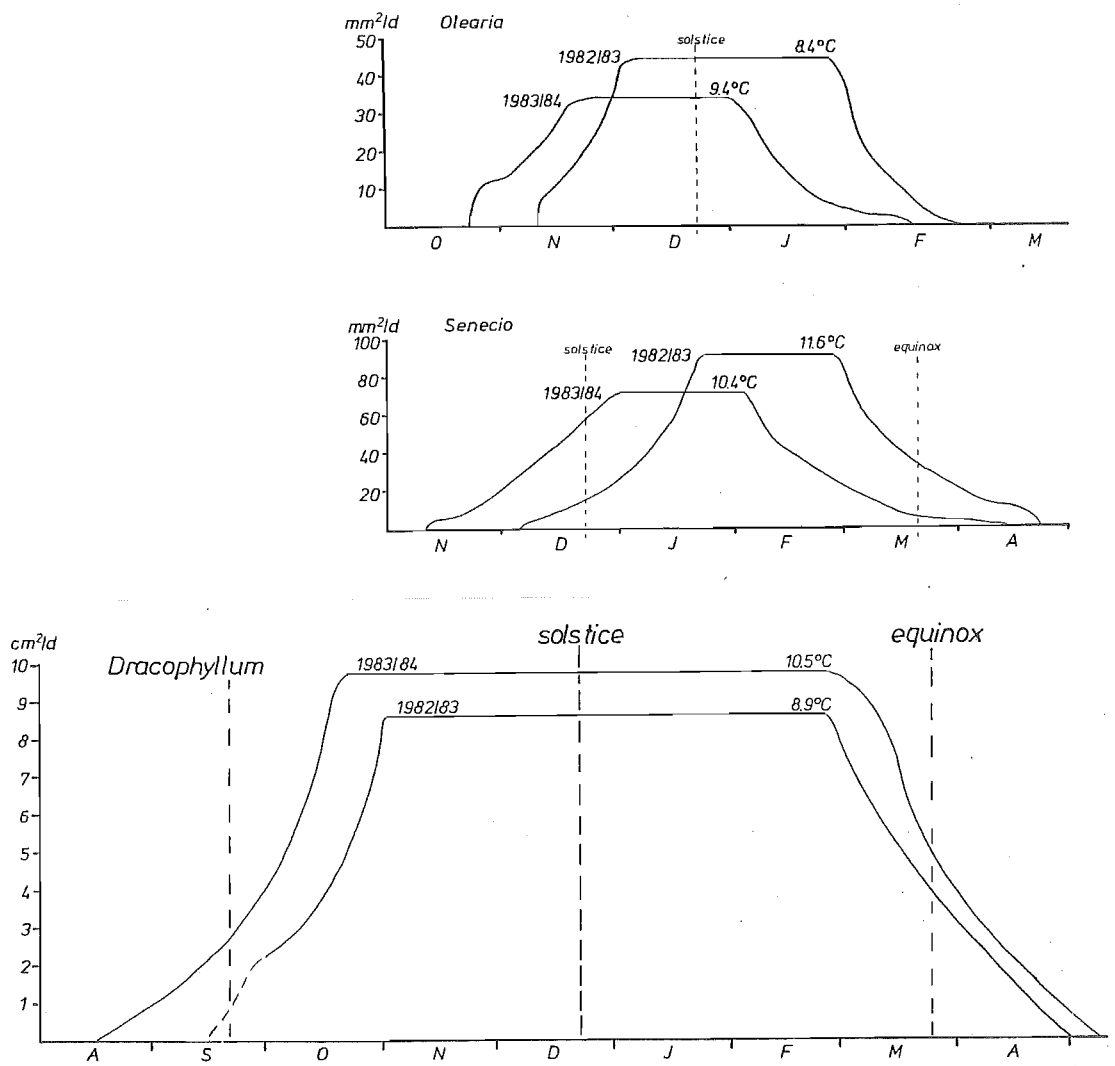

Figure 94. Seasonal variation of average daily leaf area increment (data based on interpolation from figures 53,57,61).

The 1983/84 period of leaf area growth for *Senecio bennettii* was also slightly longer than in 1982/83; nevertheless peak growth rates and total leaf area increment per shoot were at a relative minimum. In 1982/83 peak growth rates occurred later in the summer and therefore enjoyed higher temperatures because of the late start of the growing season, but the days were already becoming noticeably shorter at this time of the year. It is therefore assumed that in the two investigated composites both the total newly produced leaf area per shoot and the maximum daily increment rates are, for the most part, unrelated to the current climatic conditions. A particularly striking example is the leaf area in *Olearia ilicifolia* where the maximum falls into the 1982/83 season with far below average temperatures during the period from October to March. An absolute minimum, on the other hand, occurred in 1983/84 when temperatures were at least slightly above average.

It seems reasonable to regard the minimum of vegetative growth in 1983/84 as a result of the preceding cool 1982/83 growing season, i.e., that there was a carry-over effect. The same applies for the maximum of 1982/83, if it is regarded as a response to the warmer than average summer of 1981/82.

Many trees from the northern temperate zone have a determinate number of leaf primordia enclosed in their resting buds and only that number of leaves can be expanded during the subsequent growing season. Only some species like *Populus* or *Eucalyptus* (heterophyllous species) are able to add more leaves from currently produced primordia later in the season (e.g. Kozlowski, 1971). Bussell (1968a) de-

scribed preformed shoots with a determinate number of leaf primordia in some New Zealand trees including *Hoheria glabrata*. It is supposed that *Olearia* and *Senecio* fall into this category as well,as the variation in annual leaf production is unrelated to current climatic conditions but can be conveniently explained in terms of preformation of leaf primordia.

Kozlowski noted the influence of environmental conditions on the rate of production of leaf primordia (Kozlowski, 1971). Schwabe (1963) also comments on the environmental control of leaf initiation - though dealing with herbaceous plants - and cites experimental work (Gregory, 1921, 1928; Milthorpe, 1956; Schwabe, 1957) to stress that low temperatures at leaf initiation result not only in a smaller number of primordia per bud but also negatively affect the final size of the individual leaves.

To be able to assess the influence of environmental temperature on the rate of leaf primordia production, it is necessary to know the approximate time of leaf initiation for a given species. Bussell shed some light on this question after dissecting buds of *Hoheria glabrata, Aristotelia serrata, Fuchsia excorticata* and *Nothofagus solandri* var. *cliffortioides*. He states that in all species the first foliage leaf primordium is produced three weeks after the previous resting bud has opened. The following primordia are produced at a fast rate that soon declines and the bud is completed after six weeks in *Hoheria* and after up to six months in the other species (Bussell, 1968a).

Dates of bud break have been noted for *Hoheria, Olearia* and *Senecio* in 1982 and 1983, and with the aid of Bus-

sell's data it was attempted to determine the approximate time of leaf primordia initiation. As a rule, the time span from 3-9 weeks after bud break was considered to be most important. The mean air temperature during this period was then calculated from the daily records or by using the mean monthly temperatures from the Otira station that had been interpolated according to the altitudinal difference to cover the seasons prior to 1982/83. During the 1980/81 and 1981/82 seasons bud break was not observed in the field and the approximate date of bud break was estimated to be one week later than in 1983/84. This seemed appropriate as both September and October temperatures were comparable for all three years (1980, 1981, 1983), but the 1983/84 season was preceded by a warmer than average August which allowed for a still earlier start of the growing season.

The relationships between mean air temperature during leaf primordia initiation and the mean new leaf area per shoot in the following growing season are shown in figure 95. It was not attempted to calculate exact regression coefficients as the mean temperatures for 1980 and 1981 are only interpolated figures and the time of bud break is an approximation. Nevertheless, the results are satisfactory for this purpose. The seasonal variation in leaf area follows a different trend in *Olearia* and *Senecio* (refer to figures 54 and 58), the cause for this phenomenon is that the sensitive period for leaf primordia initiation does not coincide. In 1982 and 1983 the two respective six weeks periods had only one week overlap and both species will thus be subjected to different temperature regimes with the result that years of maximum and minimum leaf area increment are not necessarily

coincident for the two species.

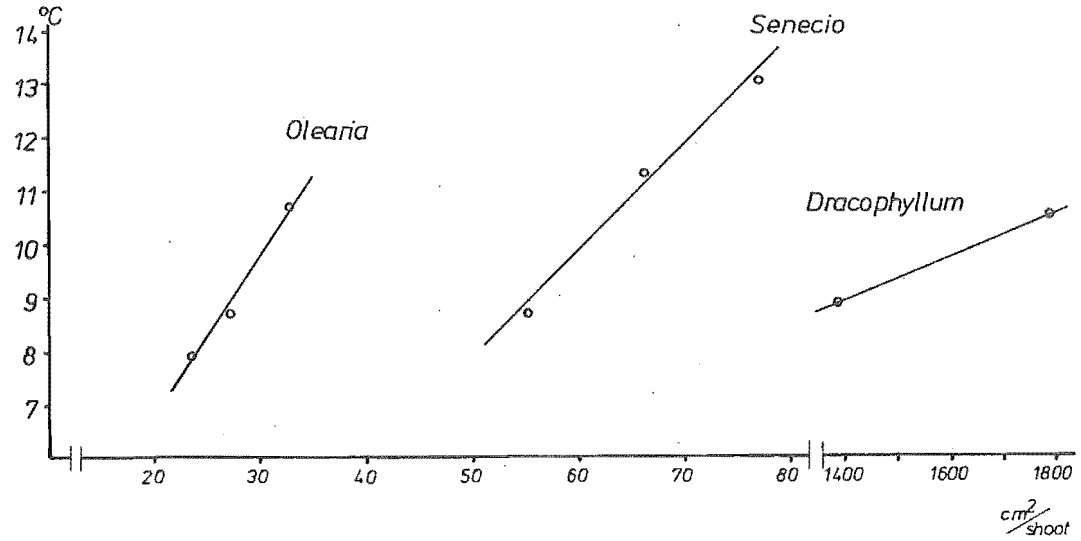

Figure 95. Relationship between average annual leaf area increment per shoot and the mean air temperature during the period of leaf primordia initiation of the previous season.

Leaf area of *Hoheria glabrata* was only determined in 1983/84, therefore no comparisons with former seasons could possibly be made, but if *Hoheria* has a determinate number of leaf primordia in the resting bud as stated by Bussell (1968) it will show the same tendency for annual variation, probably closely related to the pattern of *Olearia* as both species start growth early in the season and their sensitive periods for leaf initiation will be almost coincident.

Leaf area growth of *Dracophyllum traversii* is probably only affected by both the duration and the quality of the current growing season. It is supposed that the number of annually produced leaves is not influenced by the climatic conditions of the previous season as there are no indications for the formation of a resting bud of any kind. New leaves are produced throughout the season. Most important, however,

is the fact that the growth of currently produced leaves contributes only a negligible part towards the total annual leaf area growth. Most of it is made up by extension growth of older leaves that resume growth at the onset of the growing season. The final length and area of individual leaves varies only insignificantly and is not regulated by past or present environmental conditions.

Figure 94 shows mean daily rates of leaf area increment per shoot during the 1982/83 and 1983/84 seasons. The plateaus constitute the periods of maximum growth rates and are marked by simultaneous extension growth of the maximum number of leaves. As the oldest leaves attain their final size and no further new leaves are unfolded from the shoot apex, mean daily area increment declines, though the younger leaves will continue to grow at the same rate. Only very early or late in the season will the actual growth rate (cell division and elongation) be affected by low temperatures. In *Dracophyllum traversii* total leaf area growth is independent of the currently formed leaves, the lower growth rates in the early season will therefore be controlled by low temperature. Maximum growth rates were attained at about the 1st November, 1982 and 20th October, 1983, and it was noticed that these dates coincided with a threshold value of 7-7.5^{o}C mean weekly temperature. The decline of the growth rate in late February started immediately after the annual temperature peak (13.1^{o}C weekly mean in 1983 and 15.0^{o}C in 1984), and the ultimate cessation of leaf growth is again controlled by low temperature for it coincided in both years with the date when mean weekly temperatures dropped below about 7^{o}C.

Mean weekly temperature varied considerably during the

period of maximum increment but did not fall below 7°C for any length of time during the 1983/84 season (see diagram, appendix IV). The growth rate diagram for 1982/83 was prepared with the aid of scanty data only, therefore, possible variations could not be detected. The temperature fell below the presumed threshold value (7°C weekly mean or 10°C mean weekly maximum) on three occasions between November and January and this may be responsible for the overall slightly lower growth rate during the 1982/83 season.

A similar threshold value of 5°C seems to be related to the start of first leaf growth early in the season. Benecke et al (1978) suggested that bud break in *Nothofagus solandri* var. *cliffortioides* does not occur until mean air temperatures rise above 5°C - this can be directly compared with the start of leaf growth in *Dracophyllum traversii* which does not form resting buds - and that rapid shoot growth starts when mean air temperatures reach 7-10°C; i.e., a threshold value that compares well with the 7-7.5°C found to be related to the commencement of maximum leaf growth in *Dracophyllum traversii*.

Though comparable threshold temperatures will activate the resting buds in the other species, commencement of leaf expansion and maximum increment could not be related to the current environmental temperatures. Once the resting bud is released from dormancy, leaf growth will start after the buds have opened and then proceed until the predetermined leaf size is attained. No further growth can then take place, even if the environmental conditions are still favourable. Leaf and shoot growth and the onset of dormancy is therefore autonomously controlled because the dimensions of the shoot

are predetermined in the resting bud. This was already suggested by Bussell (1968a), who also stated that growth rates seemed to be almost independent of both temperature and day length in the species with determinate growth (Bussell, 1968b). Only temperature extremes may considerably retard growth rates.

Variation in annual shoot growth is controlled by climate as well but can not be explained with a single temperature figure. Variation in shoot length in *Olearia* and *Senecio* matches the respective pattern of variation that is exhibited by the annual leaf area figures. Observations for five seasons are available for *Hoheria glabrata* shoot growth but the pattern of variation revealed can not be matched by either the respective temperatures during the initiation period of the previous season or by the temperature during the period of rapid shoot extension growth. Though stressing that shoot growth is predetermined in the resting bud, Kozlowski (1971) also mentiones that stored carbohydrates and products of current photosynthesis are used for shoot growth. These must be considered as additional factors, the former will be dependent on the quality of the past growing season, the latter will be influenced by the environmental conditions of the current season.

Temperature has an important bearing on plant physiology. Photosynthesis is positively influenced by rising temperatures but at higher temperatures it is checked by increased respiration and transpiration (Kozlowski, 1971). Pisek and Winkler (1959) verified this with seedlings of *Pinus cembra* (a timberline species) where photosynthesis increased only up to temperatures of 10-15^{o}C but then decreased again. Climate records at Pegleg Flat revealed that daily

maximum temperatures are of a comparable value. Weekly means of the daily maximum temperature were between 10 and 15°C from mid October to mid April, i.e., throughout the growing season. All four subject species made normal progress with regard to vegetative growth and, as predominantly montane to subalpine species, they seem, like *Pinus cembra*, to be adapted to the cooler temperatures prevailing at higher altitudes.

Pisek and Tranquillini (1954) demonstrated that high light intensities caused high leaf temperatures, high respiration and a subsequent decrease in photosynthesis in crowns of *Picea excelsa* and *Fagus sylvatica*. Particularly favourable for high photosynthesis were changing light intensities and diffuse light under overcast skies. This may explain why the investigated subalpine trees and shrubs apparently did not show any noticeable variation in growth rates in reponse to periods of either cloudy or sunny weather, the former being most frequent in the superhumid subalpine environment.

Sakai and Wardle (1978) determined the freezing resistance of a variety of New Zealand trees and shrubs under experimental conditions. *Hoheria glabrata* resting buds were severely damaged at temperatures below -15°C, twigs below -17°C. For leaves , buds and cortex of *Senecio bennettii* the critical temperature was -10°C (xylem -13°C). A temperature of -10°C was also critical for the foliage of *Dracophyllum longifolium* and *Nothofagus solandri* var. *cliffortioides*, and -13°C for *Libocedrus bidwillii*, *Podocarpus hallii* and *Dacrydium biforme*, whereas *Phyllocladus alpinus* survived temperatures as low as -18 to -20°C. It should be noted that all the tested species that were hardy enough to survive tempera-

tures below -10°C are either conifers or deciduous dicotyledons. The broadleaf evergreens seem not to be adapted to extremely low temperatures, but these are not presumed to occur in their present environment.

3. FLORAL INITIATION AND FLOWERING PERIODICITY

Most studies on floral initiation and development in arboreal plants have been restricted to fruit trees. Many angiosperm trees of the temperate zone form flower primordia during the season preceding the flowering, usually during late spring to early summer (Matthews, 1963, cited by Kozlowski, 1971). The growth of the floral apex is arrested during the winter but resumes rapid development in the following spring. Flowering periodicity varies in different species; some flower annually, others are biennial, others flower at still greater intervals.

On a physiological basis, floral initiation is influenced by light intensity and associated with long days, high photosynthetic rates and high levels of nutrition, particularly high nitrogen and carbohydrate levels in the branches, in excess of the vegetative growth requirements (Shoemaker and Teskey, 1959). The ultimate control over the morphogenesis of flower primordia in the buds, however, is by way of phytohormones (Lewis, Coggins and Hield, 1964).

Annual flowering has been recorded for a number of New Zealand trees, e.g. *Weinmannia racemosa* (Wardle, 1966), *Phyllocladus alpinus* (Wardle, 1969), and *Metrosideros umbellata* (Wardle, 1971), though intensity of the flowering may vary from year to year and is less pronounced at higher altitudes in the two latter species. The flowering periodicity

of southern beech (of the *Nothofagus fusca* group) has received particular attention (e.g. Hocking, 1936; Poole, 1949; Connor, 1966; J.Wardle, 1970). Though J.Wardle stresses that there is considerable variation in seed production from year to year and seed years do not necessarily coincide throughout the geographical range of *Nothofagus solandri*, he noted that good seed years occur at about three year intervals. A three year cycle subject to slight modification caused by extreme temperatures was also recognized by Poole (1949) and Connor (1966) and was found to coincide with the flowering cycle of *Chionochloa rigida* (Connor, 1966; Mark, 1968). All authors noted that floral induction takes place at the end of particular warm and dry growing seasons and flowering then occurs during the following summer. The third season of the cycle when only vegetative growth takes place, was termed non-flowering/non-inductive by Connor (1966). A similar three year flowering cycle was also recorded for *Aciphylla aurea* and *Celmisia lyallii* (Campbell, 1981).

Records on floral initiation and flowering periodicity of New Zealand subalpine trees and shrubs, except for *Phyllocladus alpinus* and *Olearia colensoi*, are lacking so far, but data on alpine herbs are available. Mark (1970) sampled shoots of 100 alpine plants and found that at least 81 of these possessed floral primordia in autumn. He also noted an apparent lack of flower bud protection in most species, loss of primordia due to winter frost, however, was negligible. Mark notes the advantage of alpine plants possessing this flowering strategy to successfully complete their growth cycle during the short growing season at high altitudes. As preformation of flower buds has been demonstrated in both tempe-

rate zone trees and alpine plants it may be safely assumed that woody subalpines will possess the same strategy. This was proven in the case of *Dracophyllum traversii* which showed noticeably swollen terminal tufts by late March/April, and with regard to the state of development, it is assumed that the flower buds were initiated earlier than that. *Dracophyllum traversii* flowered in all four observed seasons but profusely only in 1984/85.

Axillary flower buds appear very early in *Hoheria*. Godley (1979) mentions October for trees at Lewis Pass and it must be assumed that the floral primordia have overwintered in the resting bud and were initiated during the previous season. *Hoheria glabrata* developed flower buds in all four seasons of this study as well, but almost all buds aborted and were shed during the cool and wet 1982/83 season.

Olearia ilicifolia flowered annually and flower primordia seem to be initiated in the previous season as they appear soon after the buds opens. Variation in intensity from year to year will probably depend on the prevailing temperatures during the initiation period.

Flowering of *Senecio bennettii* is more complicated because flower panicles are only born on short shoots, the number of which varies considerably from year to year. Floral initiation is thought to take place during the summer preceding the flowering as flower buds appear very early in the growing season. In certain seasons like 1981/82, when very few short shoots were formed, floral initiation does not take place in spite of favourable temperatures and no flowering occurs in the subsequent season. Flowering of *Senecio bennettii* is usually restricted to a small part of

the population, years of heavy flowering may occur periodically (like 1984/85).

Though all four investigated species may flower or at least produce flower buds annually, flowering is more common and intense in the two species with higher nutrient requirements, i.e., *Hoheria glabrata* and *Olearia ilicifolia*, whereas *Senecio bennettii* and *Dracophyllum traversii* usually bear only few flower panicles and profuse flowering occurs only periodically, probably as a result of their slower growth rates and limited nutrient supply. The same seems to apply to *Olearia colensoi* which also grows on the more mature and leached soils (Wardle, Field and Spain, 1971).

Notes on the flowering of a few more subalpine trees and shrubs at Pegleg Flat were also collected during the field study. *Olearia avicenniaefolia*, *O.arborescens* and *O. "macrodonta"* flowered annually, *O.arborescens* usually profuse. *Dracophyllum longifolium*, *D.uniflorum* and *Gaultheria crassa* flowered annually. *Pseudopanax simplex*, *P.lineare* and *P.colensoi* flowered in 1981/82 and *P.colensoi* again as early as mid August 1984. *Griselinia littoralis* flowered heavily in 1981/82 but only few trees subsequently. *Metrosideros umbellata* flowered profusely in 1982/83 and to a lesser extent in 1983/84. A number of plants were only seen flowering profusely or at least to some extent in 1981/82; *Myrsine divaricata*, *Pittosporum divaricatum*, *Coprosma pseudocuneata*, *Phormium cookianum*, *Astelia nervosa*, *Chionochloa flavescens*, and the already mentioned species of *Pseudopanax*. The 1980/81 season is therefore presumed to have been a favourable one for floral initiation. Annually flowering species, e.g. *Olearia ilicifolia*, were also affected and flowered more heavily in

the following 1981/82 season. A similarly heavy flowering season is expected in 1984/85, several of the species that did not flower since 1981/82 have already been noticed to bear flower buds.

Favourable environmental conditions during the early growing season resulting in initiation of floral primordia do not ensure the ultimate success of flowering and fruiting. The climatic regime of the flowering season proper can in several ways influence the extent of reproductive success. Flower primordia may be killed during particular hard winters, floral development may be retarded by cold and wet weather during spring and early summer. Cool and humid conditions will also prevent successful pollination in both wind and insect pollinated species. Ripening of fruits and seeds, and even dispersal of anemochorous seeds will be negatively influenced by adverse climatic conditions. The most favourable combination to ensure a heavy seed crop is a sequence of two warm or at least mild summers (and a not abnormally cold winter), the first for profuse floral initiation, the second for flower development, pollination and fruit development. The climatic records constructed for Pegleg Flat show this combination in 1980/81 - 1981/82; the heavy flowering and fruiting in the latter season seems to prove this theory. Another instance was 1973/74 - 1974/75. No records on flowering or fruiting are available for the 1974/75 season, but widespread regeneration of *Hoheria glabrata* believed to originate from a heavy 1975 seed crop, indicates that two warmer than average summers in a row will result in a particularly high seed production.

4. HABITAT AND ECOLOGICAL CHARACTERISTICS

(1) *Hoheria glabrata*

Scattered individuals of *Hoheria glabrata* occur throughout most types of subalpine forest and scrub except for the *Dacrydium biforme* forests on gley soils. These trees will serve as a seed source, and new surfaces exposed or deposited by slips, rockfalls, avalanches, etc. will soon be occupied by *Hoheria* seedlings besides other species with similar requirements, e.g. *Olearia avicenniaefolia, O.ilicifolia, Hebe salicifolia, Coprosma rugosa.* Its fast growth enables *Hoheria* to supersede the other species and it often becomes the dominant forest tree in a later stage of the succession. At certain sites where disturbance is recurrent, especially avalanche paths of deposit areas, most other species will be excluded and only *Hoheria glabrata* is able to tolerate the repeated physical damage. Another advantage for colonisation of new ground is the relatively young reproductive age of *Hoheria glabrata.* Once a few seedlings become established they will grow fast and produce the first seed crop (though of limited size) at an age of 6-8 years. The seeds will usually be dispersed in the immediate vicinity and ensure a more dense stand of *Hoheria* than would result from further chance dispersal by more distant seed sources. As compared with other subalpine species, *Hoheria* seeds possess a high viability and rate of germination, and the fast growth rate will ensure high seedling survival and establishment after germination at suitable sites.

Hoheria glabrata may germinate under a closed canopy; the seedling density is often highest under tall *Hoheria* stands. However, subsequent progress is slow and most seed-

lings die within the first three years. In places the ground cover will actually account for more shading than the forest canopy. Vegetative regeneration from dormant buds is well developed in *Hoheria* and sucker shoots may grow to 50cm or more in one year. Usually, these shoots arise after mechanical injury and enable the species to survive even when the main stem has been broken, foliage or bark has been stripped off, or after partial burial of the tree by talus.

The high nutrient requirements of *Hoheria* are reflected in the high concentrations of N, P, K, and Ca in all tissues of the species. The deciduous habit that results in a rapid loss of biomass at the end of the season, can be afforded as a "luxury" because mineral nutrients can be readily replaced by uptake of elements from the soil solution.

Compared with the broadleaf evergreen trees and shrubs of the subalpine belt, *Hoheria glabrata* has developed a life strategy that enables it to successfully exploit the high nutrient resources at disturbed sites, but is at the same time able to cope with a wide range of natural hazards that are usually associated with these locations. The high soil fertility of the preferred sites has allowed the species to adopt the deciduous habit which enables the survival of lower temperatures than the evergreen broadleaf trees and shrubs. Hoheria can therefore still maintain an erect growth habit at altitudes where all other species are reduced to shrubby growth.

The growth habit and life strategy of *Hoheria glabrata* is similar to that of certain species of *Alnus* and *Salix* in subalpine environments of the northern temperate zone. Here the domain of hardy evergreen conifers is broken by patches

of the deciduous species which are highly adapted to nutrient rich but precarious sites such as avalanche paths or flood channels.

(2) *Olearia ilicifolia*

Olearia ilicifolia has similar site requirements to *Hoheria* and groves of the latter will almost always contain a number of *Olearia ilicifolia* trees except in the most severe habitats, like avalanche areas. *Olearia*, too, shows a tendency for vegetative regeneration in response to mechanical damage, but the sucker shoots lack the vigor and growth rates encountered in *Hoheria* and will only succeed occasionally.

Regeneration from seed is, for the most part, restricted to open habitats with disturbed ground, but *Olearia* seedlings are never encountered in such high numbers as *Hoheria glabrata* seedlings though *Olearia* produces a far larger crop of seeds. Germination under a forest canopy is almost absent, possibly as a result of the light requirement, but probably also because the very small seedlings are unable to become established on the litter-covered forest floor. Abundant regeneration of *Olearia ilicifolia* was only observed on talus fans in the upper Kellys Creek catchment. Even under experimental conditions only a few of already germinated *Olearia* achenes produced healthy growing seedlings while there were no problems with *Hoheria* in this respect. *Hoheria* seedlings are thus more likely to become established at suitable spots within the more mature types of forest while *Olearia ilicifolia* is usually totally excluded from these associations.

Except for the habitat preference, there are further similarities of the life strategies of *Hoheria* and *Olearia*.

Both species start and complete their annual shoot and leaf growth at approximately the same time of the growing season, though *Hoheria* is usually slightly ahead of *Olearia*. Shoot growth ceases comparatively early in the season because the predetermined number of leaf primordia unfolds relatively fast. Although *Olearia* is evergreen its foliage is short-lived when compared with other broadleaf trees.

(3) *Senecio bennettii*

Senecio bennettii has a different growth habit from the two former species. It is an erect to decumbent shrub and has a very wide distribution within all investigated subalpine forest and scrub associations. It is, however, usually absent from the early successional scrub on disturbed sites and less common in the undergrowth of *Hoheria glabrata* dominated forests. Mixed *Hoheria/Olearia* forests, however, contain *Senecio bennettii* in the shrub layer and the species is a very important member in forest and scrub associations on the more mature soils. *Senecio bennettii* constitutes 80-90% cover of the shrub layer of the scrub vegetation in most places above timberline at Pegleg Flat. This may be a result of the late 19th century fires that destroyed part of the original subalpine low forest, and *Senecio bennettii* successfully recolonized during secondary succession.

Senecio bennettii seedlings are common in the subalpine forest associations other than pure *Hoheria glabrata* forest. Individuals that enjoy higher light intensities in canopy gaps or at the forest margin show the highest growth rates.

Flowering in *Senecio bennettii* is usually sparse, only

a small percentage of the population will produce a number of flower panicles, though some individuals may flower heavily. Reproduction means a comparatively high dry matter loss as complete short shoots will abort as a result of flowering. It is supposed that most shrubs growing on leached soils would be unable to replace this loss from current uptake and can only afford to flower more profusely in certain years after having stored sufficient carbohydrates.

The growth habit of *Senecio bennettii* which can be an erect spherical shrub in open scrubland or an erect to procumbent shrub in the forest undergrowth and at forest margins, is reminiscent of the genus *Rhododendron* in subalpine habitats of the northern temperate zone

(4) *Dracophyllum traversii*

Dracophyllum traversii is a common tree of the subalpine and upper montane belt in the NW part of the South Island. Its slow growth rate enables the species to occupy sites with leached and podzolized soils that can still sustain its nutrient demands. The foliage is long lived and litterfall restricted to the growing season. The litter, however, takes several years to decay, it accumulates on the ground and will ensure a gradual but steady return of mineral nutrients to the soil solution. The litter cover is inimical to seedlings of all kinds.

Though *Dracophyllum traversii* shows very slow growth and may attain an age of 550 years or more - a feat that is usually attributed to late successional species - the tree can appear in a very early stage of succession (especially secondary succession) when seed sources are close by. Rege-

neration in canopy gaps of the subalpine forest is only rarely encountered. The mode of seed dispersal - seeds are not adapted to wind dispersal except for their low weight and fall in high density a short distance downwind of the seed trees - is responsible for dense stands of *Dracophyllum traversii* with only a few other trees reaching the canopy.

At sites with moderate to steep slope angles that effectively prevent the soil water from stagnating, subalpine low forest dominated by *Dracophyllum traversii* and its associated species, e.g. *Libocedrus bidwillii* and *Phyllocladus alpinus*, constitutes the final stage of succession in the subalpine belt. There is, however, one decisive difference between *Dracophyllum traversii* and the "classical" late successional species (climax species in the sense of Weaver and Clements, 1938); *Dracophyllum traversii* does not sufficiently regenerate under its own canopy, partly because of the deep shade and also because of the thick and loose litter cover beneath the trees that prevents seedling establishment. Regeneration can only take place in a mosaic cycle, new seedlings become established and grow to maturity in patches of scrub in the vicinity of subalpine low forest, and only after canopy breakdown by disturbance or old age can the next generation occupy the original site. This cycle may take several hundred years or more and results in a mosaic patchwork of different subalpine forest and scrub associations. The broken terrain and the high incidence of different kinds of disturbance - earth movements, windbreak, snowbreak, etc. - that is typical for the subalpine belt of the Southern Alps, will always ensure a suitable pattern of vegetation for the successful regeneration of species with a life strategy like

Dracophyllum traversii. A similar mode of regeneration was described for *Libocedrus bidwillii* (Veblen and Stewart, 1982; Norton, 1983b) and for *Metrosideros umbellata* (Stewart and Veblen, 1982).

CHAPTER IX

CONCLUSIONS

Observations of phenology and life forms of some subalpine trees and shrubs, and available experimental data for a number of montane to subalpine tree species reveal that the present climate of the subalpine belt of the western districts of the South Island probably exerts only a mild environmental stress on the vegetation. Adaptation to cold temperatures is therefore at present not acting as a selective force. Climatological records suggest that absolute minimum temperatures of -6 to -8^{o}C occur about once a year and for a short time only. Mechanisms for bud protection during the period of winter quiescence have evolved in various ways but may be lacking altogether in certain species. In species with resting buds the buds usually contain the preformed shoot with a determinate number of leaves that expands during the following season. Bud break is dependent on rising spring temperatures and varies accordingly from year to year; species without resting buds, e.g. *Dracophyllum traversii*, can immediately resume growth as a response to rising temperatures.

In the species with preformed leaves the duration of the growing season is controlled autonomously, i.e., growth ceases after the shoot and leaves are fully expanded in mid to late summer, though wood increment may continue. In species that have not completed their growth by late summer, the resting period is thought to be induced by falling autumn temperatures rather than by short days, as proposed by Bussell (1968a,b). Above average winter temperatures allowed

continued wood increment in *Olearia ilicifolia*, a fact strongly opposed to daylength control of the growing season.

It has been suggested that the nature of the resting period in New Zealand trees is different from that of northern hemisphere species which require cold winter temperatures before the resting buds are released from dormancy (Bussell, 1968b). This low temperature requirement may be lacking or is at least present on a much smaller scale in New Zealand trees where the buds remain only quiescent as long as subjected to lower temperatures.

In the four subject species the increasing length of the individual growing season is related to decreasing soil fertility and growth rates, *Hoheria* and *Olearia* represent species on fertile sites with a short flush of growth, and *Senecio*, and *Dracophyllum* in particular, occupy sites with less fertile soils, have lower growth rates but a more extended growing season which ensures an improved competitive ability.

It is probably true that the average winter temperatures of the present climate would not necessarily impose a definite resting season on the subalpine flora of the superhumid western regions of New Zealand. Cessation of vegetative growth is controlled by falling temperatures and may serve to prevent frost damage from occasional colder than average temperatures which occur at times in the highly variable oceanic climate. It is presumed that winter dormancy, in certain cases expressed as deciduousness, evolved as a response to colder climates during the Pleistocene when winter temperatures would have exerted a selective stress on subalpine forest vegetation. A number of species were able

to adapt in morphology and phenological timing in order to avoid frost damage in winter. Deciduousness in *Hoheria* and cold hardiness in most subalpine gymnosperms are still maintained today. Other species may have been restricted to lower altitudes during the Pleistocene glacial episodes but were able to become re-established in the subalpine belt. This is indicated by species like *Pseudopanax colensoi* and *Dracophyllum traversii* which bear partly or fully developed flower buds without special protection throughout the winter.

Low incidence of deciduousness in the flora and the lack of a low temperature requirement for bud break, however, indicate that conditions during the Pleistocene were considerably less severe in the southern hemisphere with its highly oceanic climates than in the northern hemisphere. This was already suggested by Dumbleton (1967) who also referred to winter diapause in native insects.

Troll's suggestions on the seasonality of the New Zealand subalpine scrub flora were mainly based on observations of the present climate and the historical aspects of climate and flora were not considered (Troll, 1973). The growth of the trees and shrubs of the subalpine belt in the superhumid western regions is, for the most part, seasonal, but a number of species show a great deal of phenological plasticity in response to the temperatures of each individual growing season.

ACKNOWLEDGEMENTS

I wish to express my thanks to several persons and institutions for their support of various kinds.

The first year of my Ph.D. study was funded by a post-graduate scholarship for overseas studies provided by the German Academic Exchange Service (Deutscher Akademischer Austauschdienst - DAAD). I would also like to thank Prof. Dr. F.-K. Holtmeier, Institut für Geographie und Länderkunde, Westfälische Wilhelms-Universität Münster, for drawing my attention to problems of New Zealand subalpine vegetation, and, together with Prof. Dr. M. Runge (now Systematisch-Geobotanisches Institut, Universität Göttingen) for discussions and logistic support during the planning and preparation of the proposed research project.

My research at the Botany Department, University of Canterbury was supervised by Dr. Colin J. Burrows who repeatedly read the manuscript and the final version of my thesis, and who, besides advising on matters of a scientific nature, also made suggestions to improve my "German" English. Dr. David Lloyd was helpful with advice and discussion, especially during the time of my supervisor's overseas leave. Mrs. Hilary Langer suggested and discussed the use of statistical methods for the presentation of the growth measurement data and methods of vegetation analysis. Graeme Young catered for field study equipment and instrumentation and kept up the supply of laboratory chemicals. The Botany Department also provided financial assistance of various kinds.

Dr. Ian Payton, Forest Research Institute, arranged a visit of the experimental area in the Camp Creek catchment

and discussed problems of the local montane and subalpine vegetation.

The Arthur's Pass National Park Headquarters gave permission for my vegetation and soil sampling procedures; Ranger Ian Wilson advised me on suitable access routes on my occasional visits to more remote areas of the National Park.

The New Zealand Meteorological Service, Wellington, provided the necessary climatological data.

My brother Rainer assisted with the vegetation sampling procedures during the summer of 1981/82. My brother Hans successfully tackled the usually difficult problem of overseas finance transfer, not sparing his own accounts after mine had been exhausted.

At last, I would like to thank all my past and present flatmates of fifteen different nations who made living in Ilam Flats a special experience.

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A P P E N D I X I

SOIL PROFILE DESCRIPTIONS OF THE INVESTIGATED SAMPLE PITS

Profile 1 (OTR)

Location: South bank of Otira River, 50m upstream of the river bend.

Topography: level river terrace, 830m a.s.l.

Site drainage: well drained

Vegetation: Subalpine low forest dominated by *Olearia ilicifolia* and *Hoheria glabrata*

Parent rock: alluvium; greywacke pebbles and boulders

Pit description:

5.5-2.5cm	O_1	loose litter of slightly decomposed leaves, mainly of *Olearia ilicifolia*, *O."macrodonta"* and *Griselinia littoralis*
2.5-0cm	O_2	dark brown mull
0-8(12)cm	A	well rounded pebbles, spaces filled with black (10YR3/1) loamy sand with crumb structure
8-25(30)cm	B	well rounded pebbles with greyish brown (10YR3/2) loamy sand
25-65cm+	C	tightly packed subrounded boulders of 30-50cm size, spaces filled with unweathered, angular, fine gravel

Profile 2 (PLC)

Location: south bank of Pegleg Creek, about 170m E of State Highway bridge

Topography: slightly rolling river terrace, 840m a.s.l.

Site drainage: well drained

Vegetation: subalpine low forest of *Olearia ilicifolia* with some *Hoheria glabrata*

Parent rock: river alluvium, possibly with some talus from adjacent slope

Pit description:

	O_1	almost absent, only some *O.ilicifolia* litter
3-0cm	O_2	dark brown mull
0-1(2)cm	A	black brown (10YR2/1-2) stony loam with humus and nutty structure
1-50cm+	B	greyish brown (10YR5/3-4) stony clay loam with weakly developed nutty to blocky structure

Profile 3 (HGF)

Location: healed slip at the N slope of Phipps Peak, 230m E of State Highway bridge

Topography: NW facing slope, 35°, 910m a.s.l.

Site drainage: well drained

Vegetation: subalpine low forest of *Hoheria glabrata* with occasional *Olearia ilicifolia* and dense ground cover of *Polystichum vestitum*

Parent rock: moderately weathered loam from greywacke

Pit description:

	$O_{(1)}$	almost absent, scattered litter of *Hoheria*, *Olearia* and *Polystichum*
0-4(6)cm	A_1	black (10YR2/1-2) stony loam, stones subang.
4-15(17)cm	A_2	greyish brown (10YR5/4) stony loam with nutty structure
15-70cm+	B	dark yellowish brown (10YR5/6) stony loam

Profile 4 (GOT)

Location: lower NW slope of Phipps Peak, 140m SE of State Highway bridge

Topography: slightly rolling terrace, 860m a.s.l.

Site drainage: weel drained

Vegetation: open subalpine scrub dominated by *S.bennettii*

Parent rock: strongly weathered fluvioglacial deposit of greywacke boulders

Pit description:

0-4(6)cm	A_1	black brown (10YR3/1) loamy fine sand, restricted to spaces between the boulders
4-20/30cm	A_2	brownish grey (10YR5-4/2) very bouldery (90-95% vol.), loamy fine sand with very weak crumb structure
20/30-50cm+	B	brown (10YR3/3-4) very bouldery, loamy fine sand

Profile 5 (HTS)

Location: lower SW slope of Hills Peak, 100m ENE of State Highway bridge

Topography: slope of a high terrace of Pegleg Creek, 37°, 845m a.s.l.

Site drainage: well drained

Vegetation: subalpine low forest with *Dracophyllum traversii* and *Phyllocladus alpinus*

Parent rock: strongly weathered alluvium from greywacke

Pit description:

2-0cm	O	litter of dead and partly decomposed *Dracophyllum traversii* and *Blechnum capense* leaves
0-6(10)cm	A_1	dark brown (10YR3/1) stony loam
6-15cm	A_2	pale grey (10YR5/2) stony loam
15-20cm	B_1	transition zone with a colour change from grey to yellow; stony loam
20-40cm	B_2	pale orange brown (10YR6/6) stony loam
40-65cm+	B_2	grey brown (10YR6/4) very stony loam

Profile 6 (SAF)

Location: lower slope of Phipps Peak, 130m SE of State Highway bridge

Topography: straight slope with western aspect, 25°, 850m

Site drainage: temporarily waterlogged after rainfalls

Vegetation: subalpine low forest with *Libocedrus bidwillii*, *Phyllocladus alpinus* and *Dracophyllum traversii*

Parent rock: strongly weathered loam from greywacke

Pit description:

2-0cm	O	litter of *D.traversii* and *G.littoralis*
0-4(6)cm	A_1	black brown (10YR3/1) stony loam
4-12(16)cm	A_2	brownish grey (10YR5/2-3) stony loam
12-40cm	B	greyish brown (10YR5/4-6) stony loam
40-50cm	G_1	pale grey (10YR6/3-4) stony loam
50-65cm+	G_2	pale brownish yellow (10YR7/6) stony loam

Profile 7 (DTC)

Location: N slope of Phipps Peak, 350m ESE of State Highway bridge

Topography: steep slope (40°) with NW aspect, 900m a.s.l.

Site drainage: well drained

Vegetation: subalpine low forest dominated by *D.traversii*

Parent rock: strongly weathered loam from greywacke

Pit description:

(12)7-2cm	O_1	thick litter cover of *D.traversii* leaves
2-0cm	O_2	dark brown (10YR3-2/2) mor of partly to strongly decomposed *D.traversii* leaves
0-8(10)cm	A_1	black brown (10YR3/1) stony, loamy clay
8-20cm	A_2	greyish brown (10YR4/2-3) stony clay loam
20-25cm+	B	pale yellowish (10YR6/3-4) stony clay loam

A P P E N D I X II

TEXTURE ANALYSIS OF THE SAMPLED SOILS

Pit no.	sample depth	% sample weight (without stones)		% of total weight (field estimates)		soil texture
		fine soil -2mm	gravel 2-63mm	stones 63-200mm	boulders -200mm	
1	0-10cm	14.5	85.5	≈0	0	
	10-20cm	12.3	87.7	≈0	0	very gravelly
	20-30cm	30.1	69.9	≈0	0	
	30-40cm	11.7	88.3	≤5	80-90	very stony (bouldery)
	40-50cm	13.7	86.3	≤5	80-90	
2	0-10cm	n.d.	n.d.			
	10-20cm	51.6	48.4			
	20-30cm	48.9	51.1	5-10	5-10	very gravelly
	30-40cm	41.1	58.9			
	40-50cm	47.6	52.4			
3	0-10cm	n.d.	n.d.			
	10-20cm	55.7	44.3			
	20-30cm	62.9	37.1	5-10	5-10	very gravelly
	30-40cm	64.3	35.7			
	40-50cm	49.0	51.0			
4	0-10cm					
	10-20cm	90-95	5-10	5-10	90-95	very stony
	20-30cm					
	30-40cm					
5	0-10cm	n.d.	n.d.			
	10-20cm	78.9	21.1			
	20-30cm	86.9	23.1	10-20	5-10	very stony
	30-40cm	72.1	27.9			
	40-50cm	55.6	44.4	10-20	30-50	very stony (bouldery)
6	0-10cm	n.d.	n.d.			
	10-20cm	86.8	13.2			
	20-30cm	55.5	44.5	5-10	5-10	very gravelly
	30-40cm	56.8	43.2			
	40-50cm	56.4	43.6			
7	0-10cm					
	10-20cm	70-80	20-30	≤5	≤5	gravelly
	20-30cm					

A P P E N D I X III

MEAN MONTHLY TEMPERATURES AND PRECIPITATION RECORDED AT PEGLEG FLAT (SEPT. 1982 - MAY 1984)

STATION 1:	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	(1983) Y
daily mean	5.4	4.6	7.8	8.0	8.7	11.7	9.7	7.2	4.6	3.3	2.5	4.5	4.5	8.1	8.9	8.8	10.1	13.4	12.2	9.1	5.1	6.95°C
daily max.	8.7	8.1	10.6	11.4	11.6	15.5	13.1	10.4	7.3	6.1	5.3	7.8	7.0	11.9	12.9	12.1	14.3	17.7	15.3	12.3	7.8	10.1°C
daily min.	2.1	1.1	5.1	4.6	5.8	7.8	6.3	4.1	2.1	0.5	-0.4	1.0	1.9	4.4	4.8	5.3	5.9	9.0	9.2	5.9	2.4	3.6°C
daily range	6.7	7.0	5.4	7.0	6.0	7.8	6.0	6.2	5.1	4.8	5.7	6.9	5.1	7.5	8.1	6.8	8.4	8.7	6.1	6.4	5.4	6.5°C
days with screen frost	4-5	8	1	0	0	0	2	1	2	10	16	9	2	4	0	0	0	0	0	1	5	46
rainfall	303	375	952	767	724	119	791	587	882	398	490	274	750	730	486	600	584	244	393	299	305	6831mm
STATION 2:																						
daily mean	5.5	4.4	7.7	7.9	8.5	11.5	9.9	7.5	4.9	2.4	1.3	3.2	3.7	7.5	8.3	8.1	9.2	11.5				6.4°C
daily max.	8.3	7.0	9.9	10.4	10.8	14.4	12.5	9.9	6.9	4.0	3.0	5.5	5.4	10.2	10.9	10.2	12.3	14.6				8.6°C
daily min.	2.7	1.8	5.5	5.4	6.3	8.6	7.3	5.2	3.0	0.8	-0.5	0.9	2.0	4.9	5.7	6.0	6.1	8.4				4.2°C
daily range	5.2	5.2	4.0	5.0	3.9	5.2	4.8	4.7	3.8	3.0	3.5	4.6	3.4	5.3	5.6	5.2	6.2	6.2				4.4°C
days with screen frost	3	3	0	0	0	0	0	0	1	10	16	12	4	1	0	0	0	0				44

A P P E N D I X IV

CLIMATE RECORDS AT PEGLEG FLAT

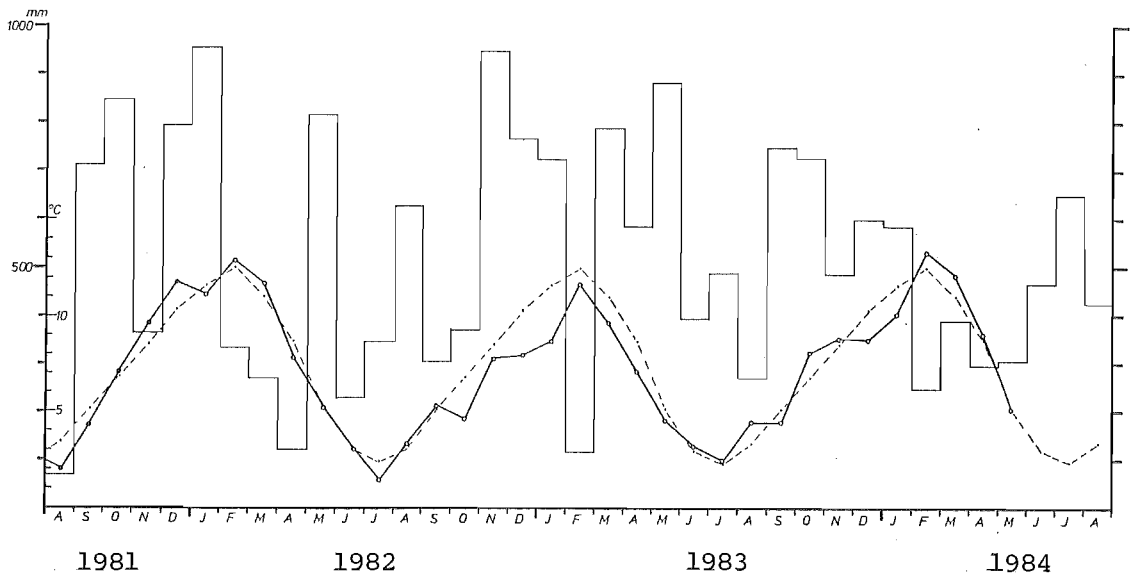

Figure 96. Monthly mean temperatures and precipitation at Pegleg Flat (1981/82 data are interpolated from Otira records).

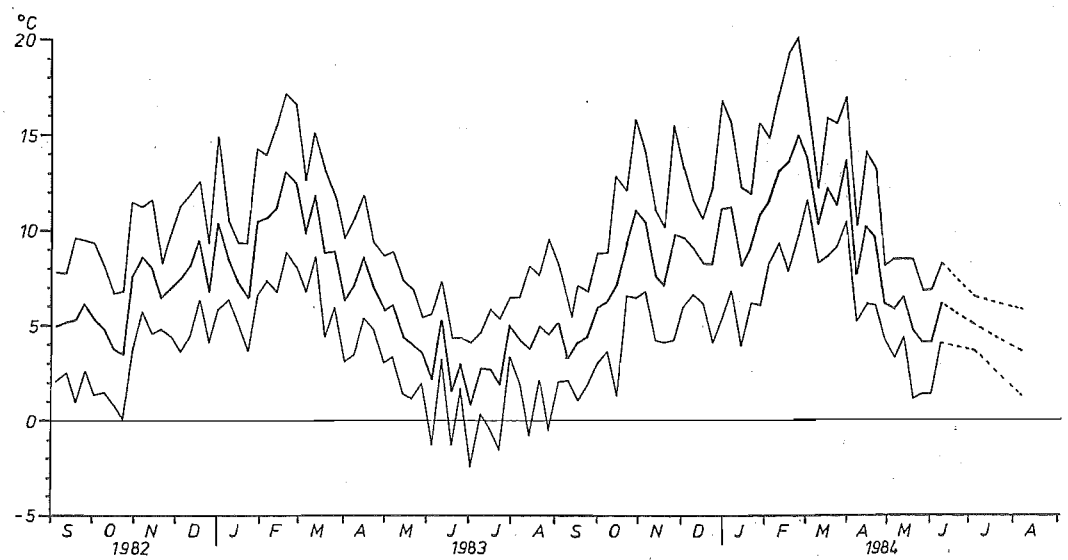

Figure 97. Variation of mean weekly temperatures during the time of observation at Pegleg Flat.

A P P E N D I X V

PERCENTAGE OF GROUND COVER IN SAMPLE PLOTS

sample plot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
total cover (%)	50	45	75	50	90	70	40	50	50	10	80	55	95	95	45	60	35	15	60	50	90	85	90	85	55	40	50	40	80	40	65	85	80	95	40
Blechnum capense	40	30	75	40	20	50	35	40	30	-	60	+	-	+	45	55	20	15	55	+	65	85	15	35	20	40	40	10	55	35	60	35	35	10	35
Polystichum vest.	10	10	-	10	70	20	5	5	5	+	20	55	90	95		5	10	+	5	25	-	+	+	-	30	-	+	-					40		+
Cyathea colensoi		-	-			-		5	-	-	-				-						5	-	-	+		-			-					
Phormium cookian.	+	+	+	+	+	+	-	+	+	-	+	+	-	-	+	+	-	+	-	+	+	+	+	+	5	+	10	10	10	5	5	10	+	10	
Astelia nervosa	+	-	+	+	+	+	+	+	5	5	-	+	-		+		+	+	-	-	+	-	5	5	-	+	+	10	-	+	-	5	+	+	
Chion.flavescens													-	-		-			-									-	+	+	-	5		10	
Ourisia macrocar.		5	+	-	+	+	+		+	-	+				+	+	-	-	+	15													+		

+, common but covering less than 5%; -,only one or two plants per sample plot